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FOREWORD

The Commonwealth Scientific and Industrial Research Organization, in collaboration with the Australian National Research Council, has decided to publish this new periodical, the Australian Journal of Botany, as a medium for the publication of results of original scientific research in botany with special emphasis on descriptive aspects.

It is not intended to issue the Journal at set periods, but as the accumulation of suitable material dictates.

THE ANATOMY OF THE TIMBERS OF THE SOUTH-WEST PACIFIC AREA

II. APOCYNACEAE AND ANNONACEAE

By H. D. Ingle[*] and H. E. Dadswell[*]

[*Manuscript received January 21, 1952*]

Summary

The results reported cover 12 genera of the family Apocynaceae and 12 genera of the Annonaceae. The anatomical features of these genera have been summarized for each family and the results compared with published information on the representatives of the families from other parts of the world. An artificial key has been developed for the separation of groups of genera in the Apocynaceae. This separation, however, does not conform with groupings based on botanical features. Possible affinities of this family have been discussed.

In the Annonaceae separation of the genera on anatomical features has been found to be difficult on account of the homogeneity in wood structure of the family as a whole.

(A) APOCYNACEAE

I. General

This family has a wide distribution mainly in tropical and subtropical areas; it covers some 175 genera, of which a number produce small to sometimes large trees. Record and Hess (1943) have referred to 30 arborescent genera from tropical America and have described the timbers of 25 of these genera. The genus *Aspidosperma* of South America has several commercially important species; the monotypic genus *Gonioma* of South Africa gives the timber known as kamassi or knysna boxwood. Three genera occurring in the south-west Pacific area provide commercially important timbers: (*a*) *Alstonia*, of which *A. scholaris* R.Br., white cheesewood, is well known in Australia, and several other species grow to a large size, producing excellent light-weight timbers; (*b*) *Dyera*, two species of which provide the well-known timber, jelutong, of Malaya and Borneo; and (*c*) *Wrightia*, of India and the Philippines, which produces fine-textured woods excellent for carving.

Metcalfe and Chalk (1950) have summarized the anatomical details of the family as a whole. In this paper the structural details of 12 genera occurring in the south-west Pacific area have been recorded; various species of some of these genera are becoming commercially important and methods for their identification are needed. As an aid to the identification of the genera examined, a key based on anatomical features has been developed.

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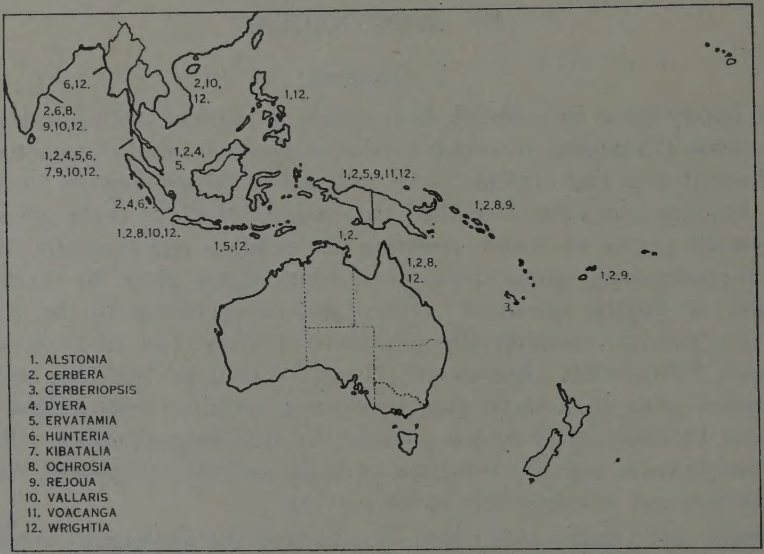
[*] Division of Forest Products, C.S.I.R.O., South Melbourne.

Of the genera available for study the tangential surfaces of the wood in *Alstonia, Cerbera, Cerberiopsis, Dyera, Ervatamia, Rejoua, Vallaris,* and *Voacanga* show a number of lenticular or slit-like openings frequently occurring in horizontal series. These openings may be 2-4 in. apart and are commonly half an inch or more high (see Plate 6, Fig. 3); they are the cross sections of radial passages running outwards from the pith. They have been described in detail by various workers, and Eggeling and Harris (1939) have suggested the descriptive term "latex traces," as they have their origin in traces from the leaves and axial buds and are characterized by the presence of latex tubes in the tissue in the initial stages. In dry, mature timber the latex traces contain only the shrivelled remains of the unlignified tissue that originally filled them; in sawn timber these generally become detached from the secondary wood.

The apparent absence of heartwood from many of the genera, notably *Alstonia* and *Dyera,* is another feature of note in the timbers of this family. Living parenchyma cells have been found right to the pith of large trees of *Alstonia scholaris* (Chattaway 1952) and starch is commonly present in the cells. Desch (1941) has recorded similar results for freshly felled logs of *Dyera costulata* Hook.f. The presence of tension wood indicated by gelatinous fibres is a common feature of several genera including *Cerbera, Cerberiopsis, Rejoua,* and *Voacanga.*

The distribution in the south-west Pacific area of the genera examined is shown in Figure 1.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3.
1. ALSTONIA
2. CERBERA
3. CERBERIOPSIS
4. DYERA
5. ERVATAMIA
6. HUNTERIA
7. KIBATALIA
8. OCHROSIA
9. REJOUA
10. VALLARIS
11. VOACANGA
12. WRIGHTIA

Fig. 1.—Distribution of genera of Apocynaceae examined from the south-west Pacific.

II. Anatomical Characteristics of the Genera Examined

Standard macroscopic and microscopic examinations of all available wood specimens of the various species were carried out and the results summarized.

Species summaries were utilized in preparing generic descriptions and the details of anatomical features for the genera have been set out in Table 2. Note has been taken of published information on any of the species examined.

(*a*) *Alstonia*

(i) *General.*—A genus consisting of some 30 species of trees and shrubs occurring throughout the Indo-Malayan region, the Philippines, New Guinea, Polynesia, and northern Australia. One species, *A. congensis* R.Br., is found in Africa (Eggeling and Harris 1939). The genus is not represented in the New World. Tree species are medium-sized to large, 80-130 ft. high. The timbers are straw-coloured to pale yellow-brown, with little or no distinction in colour; light to moderately heavy; soft to moderately hard; generally straight-grained and fine to medium-textured. Few of the species are of commercial importance at present except *A. scholaris*, which when suitably treated to prevent attack by the *Lyctus* borer, may be used for general interior finish, furniture, cases, and veneer; it is also a good pattern-making and carving timber; latex traces (Plate 6, Fig. 3), however, are common and constitute a major defect. Some of the more dense species should, when better known, prove suitable for various uses.

(ii) *Structure.*—*Growth rings* generally not evident, sometimes marked indistinctly in denser species by somewhat thicker-walled fibres. *Vessels* small and indistinct to the naked eye to intermediate in size; maximum tangential diameters from 70 μ (*A. constricta* F.Muell.) to 220 μ (*A. scholaris*) (Plate 2, Fig. 4); mean member length 620-1060 μ; few (2-3/sq. mm.) to numerous (20 + /sq. mm.); solitary, varying from 10 to 65 per cent. in different species and in radial multiples usually 4-6 but occasionally up to 10 and often in small clusters; perforation plates simple, oblique with a prominent rim; inter-vessel pitting small, bordered, alternate, vestured. *Rays* 1-4-seriate, generally 2-3-seriate; uniseriate rays few; generally up to 30 cells high, sometimes higher; weakly heterogeneous in most species with marginal cells of greater vertical dimensions than the central though seldom upright; some rays distinctly heterogeneous in *A. verticillosa* F.Muell. with 1-3 rows of upright cells, sometimes disjunctive; horizonal latex tubes common in three species (Table 1, group I, and Plate 3, Fig. 3); chambered crystals moderately abundant in the central ray cells (Plate 4, Fig. 4) of species without latex tubes; vessel-ray pitting half-bordered, similar in size to inter-vessel pitting (Plate 3, Fig. 1), sometimes unilaterally compound. *Parenchyma* abundant apotracheal, diffuse or in fine, numerous, short, discontinuous lines one cell wide in species with smaller pores (Plate 1, Fig. 2), in remainder as fairly closely spaced bands 2-6 cells wide; paratracheal parenchyma sparse or wanting; chambered crystal strands abundant in many species. *Fibres* thin-walled to thick-walled, non-septate, pits small, numerous, and distinctly bordered; mean fibre length varying from 1.20 to 1.76 mm.

(iii) *Material.*—*Alstonia angustiloba* Miq., two samples North Borneo; *A. constricta* F.Muell., one sample east Australia; *A. constricta* F.Muell. var. *mollis* F.M.Bail., one sample north-east Australia; *A. longissima* F.Muell., one sample

New Guinea; *A. macrophylla* Wall., six samples Borneo, New Guinea, and Philippine Is.; *A.* sp. aff. *macrophylla* Wall., one sample New Guinea; *A. scholaris* (L.) R.Br., 17 samples Malaya, Philippine Is., New Guinea, Solomon Is., and Australia; *A. spathulata* Bl., one sample North Borneo; *A. spectabilis* R.Br., three samples Solomon Is.; *A. subsessilis* Miq., two samples New Guinea; *A. verticil-*

TABLE 1

ARTIFICIAL GROUPING OF SPECIES OF THE GENUS *ALSTONIA* OCCURRING IN THE SOUTH-WEST PACIFIC AREA

Species	Group I* *A. angustiloba* *A. scholaris* *A. spathulata*	Intermediate But With Closer Affinities to Group I *A. verticillosa* (syn. *A. actinophylla*)	Group II *A. constricta* *A. constricta var. mollis* *A. longissima* *A. macrophylla* *A. spectabilis* *A. subsessillis* *A. villosa*
Ray type	1-2-seriate occasionally up to 3; cells thin-walled, with intercellular spaces	1-3-seriate, cells thin-walled with intercellular spaces	1-4-seriate, cells normal in shape and wall thickness, no intercellular spaces
Latex tubes	+	+	−
Crystals	−	−	+ chambered in procumbent cells
Vessel size	Max. tangential diameter 150-220μ	Max. tangential diameter 160-180μ	Generally less than 120μ max. tangential diameter (occasionally up to 150μ)
Vessel no./sq. mm. ..	Mainly 2-5/sq. mm. (occasionally up to 10)	5-7/sq. mm.	11-20+/sq. mm.
Vessels in radial multiples	Generally 2-3 but occasionally up to 5, few clusters	2-4, occasionally up to 8, with few clusters	Frequently in long radial multiples up to 8 or 10
Parenchyma distribution	Fairly regularly spaced bands 1-2 cells wide	Numerous regular bands 2-5 cells wide	Mainly diffuse with some tendency to a short reticulate arrangement
Fibres	Thin-walled	Moderately thin-walled	Thick-walled
Density air-dry ..	20-28 lb./cu. ft.	30-35 lb./cu. ft.	35-50 lb./cu. ft.

* The African species *A. congensis* R.Br. falls into this group.

losa F.Muell. (syn. *A. actinophylla* K.Schum.), six samples north Australia; *A. villosa* Bl., seven samples New Guinea and Solomon Is.; *A.* sp. unassigned, two samples New Guinea.

(iv) Examination of the above material from 13 species reveals certain divergences and it has been possible to split the genus into two distinct groups on the basis of pore size and number, ray type, the presence or absence of latex tubes, and the parenchyma distribution. Metcalfe and Chalk (1950) mention that the species of this genus, like those of *Aspidosperma* from South and Central America, differ more than is usual within a genus. Table 1 summarizes the salient points of distinction between the two groups.

An opportunity was afforded of examining the root wood of *Alstonia spathulata,* a species that grows under swampy conditions in Malaya and North Borneo; this root wood is extremely soft and light (approx. 3 lb./cu. ft.) and is used in the making of pith helmets. It reveals certain modifications from the stem wood (Plate 6, Figs. 1 and 2), chiefly in the fibres, which show an increase in tangential diameter, from 35-40 μ in stem wood to 85-90 μ in root wood, and are approximately the same length as the vessel members in both stem and root (0.45-0.71 mm.). They also show considerable resemblance to vessel members in their shape (Plate 6, Fig. 4) and the vesturing of their pits. The vessels are fewer in number than in the stem (root less than 1 per sq. mm.; stem 7-10 per sq. mm.) and are somewhat smaller in tangential diameter; they are mainly solitary or in pairs rather than in radial multiples of 2-5 or 6 as in the stem wood. The rays show little modification and have latex tubes as in the stem. Parenchyma bands are reduced in number and irregularly spaced.

(*b*) *Cerbera*

(i) *General.*—A small genus of trees represented by some six species in the Malayan region, New Guinea, Solomon Is., and north Australia. The trees are usually small but sometimes medium to large, up to 100 ft. high. Material from four species has been examined. The timbers are straw to pale yellow-brown, with little distinction in colour from pith to bark; light to moderately light, and fine-textured. Latex traces were observed in material of this genus. The timbers, with one exception, have little or no commercial importance but could possibly be used for cases and interior construction; *C. dilatata* Mgf. has been used to some extent locally.

(ii) *Structure.*—Growth rings sometimes marked by bands of parenchyma apparently terminal or initial. *Vessels* small and indistinct to the naked eye; maximum tangential diameters 110-130 μ; mean member length 750-950 μ; evenly distributed or sometimes with more or less marked tendency to radial alignment; moderately numerous (6-16 per sq. mm.); solitary pores 20-23 per cent. of total, remainder in short to long radial multiples, usually 2-7 (Plate 2, Fig. 1) but occasionally (*C. floribunda* K.Schum.) in long radial chains up to 10 or 12, clusters common (Plate 2, Fig. 2); perforation plates simple, oblique with wide rim (Plate 3, Fig. 4); inter-vessel pitting small, bordered, alternate, vestured. *Rays* mainly 1-2-seriate (Plate 5, Fig. 1), very occasionally up to 3;

low, up to 25 cells, appearing heterogeneous in tangential section, but seen on radial sections to be composed of small central cells with marginal cells of greater vertical dimensions and only a single file of upright cells on the upper and lower margins; vessel-ray pitting small, half-bordered, and similar to the inter-vessel pitting; no latex tubes observed, but reported by Metcalfe and Chalk (1950); crystals absent. *Parenchyma* chiefly in apotracheal bands 2-8 cells wide (Plate 2, Fig. 2), varying in spacing between species and within one sample; paratracheal parenchyma sparse to almost completely vasicentric (*Cerbera* sp. unassigned); crystal strands moderately abundant. *Fibres* non-septate, thin-walled, pits indistinctly bordered; mean length 1.25-1.45 mm.

(iii) *Material.—Cerbera dilatata* Mgf., one sample north Australia; *C. floribunda* K.Schum., four samples New Guinea; *C. manghas* L., three samples Indonesia, New Guinea, and north Australia; *C.* sp. unassigned, one sample New Guinea.

(*c*) *Cerberiopsis*

(i) *General.*—A monotypic genus confined to New Caledonia. The trees are not large and apparently of no commercial importance. The heartwood is a definite brown to dark brown in colour, distinct from the pale cream-coloured sapwood; moderately dense, fine and uniform in texture.

(ii) *Structure.—Growth rings* generally indistinct. *Vessels* small and indistinct to the naked eye; maximum tangential diameters up to 120 μ; mean member length 750 μ; evenly distributed, characteristically arranged in long radial multiples or chains, sometimes up to 12, generally 2-8, with a few clusters; tendency for occasional radial or oblique alignment of pore multiples; up to 10 per cent. solitary; moderately numerous (16-18 per sq. mm.); perforation plates simple; inter-vessel pitting small, bordered, alternate, vestured; occasional white chalky deposits observed. *Rays* mainly uniseriate to partly biseriate; low, up to 15 cells; practically homogeneous; vessel-ray pitting half-bordered and similar to inter-vessel pitting. *Parenchyma* sparse, paratracheal, and in irregularly spaced bands 2-3 cells wide, not numerous; crystal strands not observed. *Fibres* moderately thick-walled, non-septate with numerous small but distinctly bordered pits; mean length 1.23 mm.

(iii) *Material.—Cerberiopsis candelabra* Vieill. ex Panch. et Seb., one sample New Caledonia.

(*d*) *Dyera*

(i) *General.*—A small genus of trees recorded from the Malayan region; three species have been recognized and material covering two of these species has been examined. The trees are very large, up to 150 ft. in height. The timber is pale-coloured, pinkish when first cut, straw-coloured to yellow-brown after exposure, indistinguishable from the sapwood; light in weight, straight-grained, and fissile. Latex traces were observed in both species of this genus. The timbers are generally useful with good machine properties suitable for interior finish, and for pattern-making. Restrictions on felling, owing to the value of the tree for latex, make for short supply (Desch 1941).

(ii) *Structure.—Growth rings* inconspicuous. *Vessels* moderately small to moderately large, visible to distinct to the naked eye; maximum tangential diameters 120-205 μ; mean member length 920-970 μ; generally not numerous (2-3 per sq. mm.), evenly distributed; solitary pores varying from 14 to 27 per cent., remainder in radial multiples of 2-4 and in small clusters; perforation plates simple and oblique; inter-vessel pitting small to medium, bordered, alternate, vestured, diameter of borders 6-8 μ. *Rays* 1-4-seriate and 25-40 cells high; heterogeneous with 1-3 rows of upright marginal cells, cells disjunctive; latex tubes present (Plate 3, Fig. 2); sometimes quite enlarged; vessel-ray pitting half-bordered, similar to inter-vessel pitting; crystals not observed. *Parenchyma* abundant, apotracheal, diffuse, and in fine, wavy, discontinuous lines forming a reticulum; cells disjunctive; crystals not observed. *Fibres* non-septate, thin-walled, pits numerous on radial walls, distinctly bordered and with vertical, slit-like, sometimes extended apertures (Plate 5, Fig. 3); mean length 1.80-1.95 mm.

(iii) *Material.—Dyera costulata* Hook.f., five samples Malaya, North Borneo; *D. lowii* Hook.f., two samples Indonesia, North Borneo.

(*e*) *Ervatamia*

(i) *General.*—A genus of shrubs or small trees confined to the tropics of the eastern hemisphere from Madagascar to the Solomon Is. Samples from two tree species were available for examination. The wood is cream to yellowish brown in colour; moderately light and soft; straight-grained and fine-textured. The timber is of no commercial importance. Many of the species contain a poison in the fruits and the bark.

(ii) *Structure.—Growth rings* inconspicuous. *Vessels* small and indistinct to the naked eye; maximum tangential diameter 76 μ; mean member length 550-970 μ; very numerous (20 + per sq. mm.); evenly distributed; 28 per cent. solitary, remainder in radial multiples of 2-10 (Plate 1, Fig. 3); inter-vessel pitting small, bordered, alternate, vestured; perforation plates simple. *Rays* of two widths (Plate 5, Fig. 2); uniseriate rays composed of upright cells, and multiseriate 3-5-seriate with margins of upright cells, which on tangential section often appear as wide as the procumbent portion; clusters of large and small crystals common in upright cells (Plate 4, Fig. 3), also distended cells, resembling oil cells; vessel-ray pitting small, half-bordered, similar to inter-vessel pitting; no latex tubes observed. *Parenchyma* sparse paratracheal to absent. *Fibres* septate with extremely fine septa; with small, inconspicuous, indistinctly bordered pits; mean length 0.96-1.50 mm.

(iii) *Material.—Ervatamia orientalis* (R.Br.) Mgf., one sample New Guinea; *E. punctulata* (Warb.) Mgf., one sample New Guinea.

(*f*) *Hunteria*

(i) *General.*—A small genus of trees represented by one species in the Indo-Malayan region, *H. zeylanica* (Retz.) Gaud., which is only a medium-sized tree. The heartwood is yellowish brown (brown with an olive-green tinge

(Desch 1941)), and not distinct from the sapwood, heavy to moderately heavy with a somewhat wavy grain, texture fine. The wood is said to be excellent for carving and is used for inlay and small articles (Desch 1941), and should prove a good boxwood substitute.

(ii) *Structure.—Growth rings* absent or ill-defined. *Vessels* extremely small, invisible to the naked eye; maximum tangential diameter 70 μ; mean member length 820 μ; very numerous (20 + per sq. mm.), entirely solitary (Plate 1, Fig. 1); perforation plates simple, oblique; vessel pitting small, bordered, alternate, vestured. *Rays* 1-4-seriate; heterogeneous; tending to be of two widths, the uniseriate composed entirely of upright cells, the multiseriate 2, 3, or occasionally 4, cells wide, having uniseriate margins of 3 or more rows of upright cells; vessel-ray pitting small, half-bordered, and similar in size to vessel pitting; no latex tubes observed. *Parenchyma* abundant, apotracheal, diffuse or tending to be in short, wavy, uniseriate lines; no crystals observed. Fibres thick-walled, non-septate, with numerous small but distinctly bordered pits on both tangential and radial walls; mean length 1.54 mm.

(iii) *Material.—Hunteria zeylanica* (Retz.) Gaud., one sample Malaya.

(g) *Kibatalia*

(i) *General.*—A small genus of trees, one species of which recorded from Malaya is *K. arborea* (Bl.) G.Don., a small to medium-sized tree. The wood is cream to pale yellow, moderately light in weight, straight-grained, and fine-textured; without odour. Nothing is recorded of the uses of the timber.

(ii) *Structure.—Growth rings* ill-defined. *Vessels* small and indistinct to the naked eye; maximum tangential diameter 120 μ; mean member length 720 μ; evenly distributed, moderately numerous (6-7 per sq. mm.); arranged in radial multiples up to six and occasional clusters; up to 20 per cent. solitary; perforation plates simple, usually oblique; inter-vessel pitting small, bordered, alternate, vestured. *Rays* 1-3 cells wide, rarely up to 4 cells, up to 45 cells high, distinctly heterogeneous with several rows of marginal upright cells; vessel-ray pitting small, half-bordered, and similar in size to inter-vessel pitting; no latex tubes or crystals observed. *Parenchyma* abundant, apotracheal, diffuse to reticulate in fine, irregular, short, uniseriate lines, sometimes 2 cells wide; chambered crystal strands present. *Fibres* thin-walled with moderately numerous, small, but distinctly bordered pits; mean length 1.27 mm.

(iii) *Material.—Kibatalia arborea* (Bl.) G.Don., one sample Malaya.

(h) *Ochrosia*

(i) *General.*—A small genus of some 15 species occurring from Madagascar to Polynesia; material from one unassigned species was available for examination. The wood of this species is cream to pale yellow in colour; fine and uniform-textured, moderately light; the timbers from two Malayan species, although small and not plentiful, are used locally; the wood of the species examined should be suitable for turnery and carving.

(ii) *Structure.—Growth rings* not evident. *Vessels* small and indistinct to the naked eye; maximum tangential diameter 110 μ; mean member length 1240 μ; evenly distributed, extremely numerous (20-40 + per sq. mm.); predominantly solitary (90-95 per cent.), with few radial or tangential pairs; vessel pitting fine, bordered, alternate, vestured; perforation plates simple, usually oblique. *Rays* tending to be of two types, uniseriate, consisting exclusively of upright cells, and triseriate with many rows of marginal upright cells; chambered crystals present in central procumbent portion of ray; vessel-ray pitting small, half-bordered, and similar to vessel pitting; latex tubes not observed. *Parenchyma* abundant, apotracheal, diffuse, tending to form short, irregular, uniseriate lines; chambered crystal cells present among strands. *Fibres* non-septate, with distinctly bordered pits; mean length 1.90 mm.

(iii) *Material.—Ochrosia* sp. unassigned, one sample New Georgia, Solomon Is.

(*i*) *Rejoua*

(i) *General.*—A small genus of trees and shrubs that produce a poor-quality resinous rubber. This genus has been split off from the genus *Tabernaemontana*; it is found in the Indo-Malayan region to Melanesia; two species were available for examination. The trees are small and the timbers of no commercial importance. Woods pale brown in colour, moderately light, straight-grained, and with a fine texture.

(ii) *Structure.—Growth rings* indistinct. *Vessels* extremely small, invisible to the naked eye; maximum tangential diameter 55 μ; mean member length 890-920 μ; evenly distributed and numerous (20 + per sq. mm.); arranged in radial multiples commonly up to 8 or sometimes 10, few solitary; perforation plates simple, oblique; inter-vessel pitting small, bordered, alternate, vestured. *Rays* 1-4-seriate, extremely heterogeneous with many rows of vertically elongated marginal cells in palisade arrangement (Record 1934); tending to two distinct widths, uniseriate of upright cells, and multiseriate of 3-4 cells wide in the procumbent portion with tall, uniseriate margins of upright cells; slightly distended cells, containing oily or mucilaginous substances and suggesting oil cells common among the upright ray cells (Plate 4, Fig. 2); no latex tubes observed; vessel-ray pitting small, half-bordered, and similar to inter-vessel type. *Parenchyma* apparently absent. *Fibres* septate and containing numerous large, elongated crystals (Plate 4, Fig. 1); frequently gelatinous; pitting inconspicuous, simple; mean length 1.38-1.42 mm.

(iii) *Material.—Rejoua anguinea* Hemsl., one sample Bougainville; *R. aurantiaca* Gaud., one sample New Guinea.

(*j*) *Vallaris*

(i) *General.*—A genus of climbers or small trees of tropical Asia and Malaysia, cultivated mainly for their flowers. *V. maingayi* Hook.f. is a small to medium-sized tree found in Malaya. The wood is straw-coloured to pale yellow, moderately light, straight-grained and fine-textured; without odour; latex traces present.

(ii) *Structure.—Growth rings* inconspicuous, sometimes marked by denser bands of fibres. *Vessels* small and indistinct to the naked eye to intermediate in size; maximum tangential diameter 145 μ; mean member length 800 μ; moderately numerous (6-12 per sq. mm.), arranged in radial multiples of 2-5 with a few clusters, up to 20 per cent. solitary; perforation plates simple, oblique; inter-vessel pitting small, bordered, alternate, vestured, diameter of borders 4-5 μ; tyloses absent. *Rays* mainly 1-2-seriate, occasionally up to 3 cells wide, varying in height, maximum 45 cells; heterogeneous with one to several rows of marginal upright cells; no latex tubes observed; vessel-ray pitting small, half-bordered, and similar in size to inter-vessel pitting, sometimes unilaterally compound; no crystals observed. *Parenchyma* abundant, apotracheal, in fine, wavy, closely spaced, uniseriate lines; chambered individual parenchyma cells containing crystals common. *Fibres* thin-walled, non-septate, pits small but distinctly bordered; mean length 1.24 mm.

(iii) *Material.—Vallaris maingayi* Hook.f., two samples Malaya.

(*k*) *Voacanga*

(i) *General.*—A genus of some 20 species of trees and shrubs from Africa to Malaysia and New Guinea. The wood of *V. papuana* is cream or pale straw-coloured, moderately light and soft, straight-grained, and fine-textured. Latex traces present.

(ii) *Structure.—Growth rings* wanting or inconspicuous. *Vessels* small and indistinct to the naked eye and very numerous (20 + per sq. mm.); maximum tangential diameter 108 μ; mean member length 850 μ; evenly distributed, up to 35 per cent. solitary but generally in radial multiples of varying length, generally up to 5, but occasionally up to 10 in one sample; perforation plates simple; inter-vessel pitting small, bordered, alternate, vestured. *Rays* 1-5 cells wide and up to 35 cells high; extremely heterogeneous with numerous rows of upright cells of palisade type; tending to be of two widths, the uniseriate composed of upright cells and the multiseriate 3-5 cells wide with uniseriate margins appearing on tangential section as wide as the multiseriate portion; sheath cells are a marked feature of one sample; distended cells resembling oil or mucilage cells observed in upright cells of one sample; elongated crystals common in marginal upright cells of rays; procumbent cells often chambered and containing crystals (Plate 4, Fig. 4); vessel-ray pitting small, half-bordered, and similar in size to inter-vessel pitting; no latex tubes observed. *Parenchyma* apparently absent. *Fibres* septate, with inconspicuous simple pits; occasionally containing elongated crystals similar to those of the upright ray cells; mean length 1.60 mm.

(iii) *Material.—Voacanga papuana* (F.Muell.) K.Schum., three samples New Guinea.

(*l*) *Wrightia*

(i) *General.*—A genus of some 14 species of shrubs or small to medium-sized trees occurring in the Indo-Malayan region, Siam, Philippine Is., New Guinea, Solomon Is., and northern Australia. Material of five tree species was available for examination, two of which, *W. millgar* F.M.Bail. and *W. tinctoria* R.Br., attain heights up to 120 ft., though they are described generally as short-boled trees. The wood of these species is of pale straw to cream colour, darkening slightly on exposure, light to moderately light; fine-textured, straight-grained, or sometimes wavy; without odour or taste; recommended generally as excellent carving timbers or for turnery (Reyes 1938).

(ii) *Structure.—Growth rings* inconspicuous to sometimes distinct owing to thicker-walled fibres. *Vessels* small and indistinct to the naked eye; maximum tangential diameters ranging from 79 to 110 μ in different species; mean member length 400-510 μ; numerous (11-20 per sq. mm.), evenly distributed, arranged in radial multiples up to 6, with few clusters, remainder up to 25 per cent. solitary; perforation plates simple; inter-vessel pitting small, bordered, alternate, vestured. *Rays* mainly 1 or 2 cells wide, occasionally up to 3, generally low, up to 25 cells high; heterogeneous with several rows of upright marginal cells, cells disjunctive (Plate 5, Fig. 4); on tangential section the uniseriate portion appearing as wide as the biseriate; crystals common in procumbent cells, chambered or subdivided; vessel-ray pitting small, half-bordered, similar in size to the inter-vessel pitting; no latex tubes observed. *Parenchyma* inconspicuous macroscopically, but abundant apotracheal, diffuse or finely reticulate in short uniseriate lines; no crystals observed. *Fibres* non-septate, with numerous small bordered pits; mean length 0.93-1.20 mm.

(iii) *Material.—Wrightia calycina* A.DC., one sample Philippine Is.; *W. millgar* F.M.Bail., five samples New Guinea, north Australia; *W. saligna* F.Muell., one sample north Australia; *W. tinctoria* R.Br., one sample New Guinea; *W. tomentosa*, one sample Siam.

III. Discussion of Results

The anatomy of the genera studied reveals the following distinctive features:

(*a*) Vessel pitting uniformly very small to small (diameter of borders 4-8 μ), alternate, vestured.

(*b*) Vessel-ray pitting constantly similar to the vessel pitting, frequently unilaterally compound and present in all ray cells in contact with vessels; Chattaway (1949) has reported the absence of tyloses in the heartwood of species when the size of aperture of vessel-ray pits is less than 10 μ.

(*c*) Non-septate fibres usually with small, but distinctly bordered pits in nine genera; septate fibres in three genera.

(*d*) Rays generally heterogeneous (except in *Alstonia* and *Cerberiopsis*), often markedly so, with a tendency to two types; uniseriate of upright cells, and multiseriate, 3-5 cells wide with many rows of marginal upright cells; cells frequently disjunctive.

(*e*) Parenchyma variable between genera; sparse to absent in genera with septate fibres, exclusively apotracheal in the majority of genera, generally diffuse to reticulate or in bands 1-3, sometimes up to 6, cells wide;

TABLE 2

SUMMARY OF ANATOMICAL CHARACTERISTICS OF 12 GENERA OF THE APOCYNACEAE OCCURRING IN THE SOUTH-WEST PACIFIC AREA

Genera	No. of Species Examined	Vessels			Rays					Parenchyma					Fibres		
								Crystals									
		Percentage Solitary	Radial Multiples of 8 or more	Max. Tangential Diameter (μ)	Predominant Ray Width (No. of cells)	Marginal Upright Cells 3 or More	Latex Tubes	Marginal	Central	Paratracheal	Diffuse	Reticulate	Apotracheal Bands	Crystal Strands	Septate	Pits Distinctly Bordered	Latex Traces
Alstonia I	4	10-25	—	150-220	1-2	—	+	+ (occas.)	—	—	—	+	+	+	—	+	+
Alstonia II	8	25-65	+ (occas.)	70-120	1-4	—	—	—	+	—	+	+	—	+	—	+	+
Cerbera	3	20-23	+	110-130	1-2 (3)	+	—	—	—	+	—	—	+	—	—	+	+
Cerberiopsis	1	5	+	120	1 (2)	—	—	—	—	+	+	—	+ (sparse)	—	—	+	—*
Dyera	2	18-24	—	120-205	1, 2-4	+	+	—	—	—	—	+	—	—	—	+	—*
Ervatamia	2	28	+	76	1, 3-5	+	—	+	—	+ (sparse)	—	—	—	—	+	—	+
Hunteria	1	100	—	70	1, 3-4	+	—	—	—	—	+	+	—	—	—	+	—
Kibatalia	1	19	— (up to 6)	120	1-3	+	—	—	—	—	+	+	—	+	—	+	—
Ochrosia	1	90-95	—	110	1, 3	+	—	—	+	—	+	+	—	—	—	+	—
Rejoua	2	20-30	+	55	1, 3-4	+	—	—	—	—	—	—	—	—	+†	—	+
Vallaris	1	16	— (occas. —5)	145	1-2 (3)	+	—	—	—	—	—	+	—	—	—	+	+
Voacanga	1	37	+	108	1, 3-5	+	—	+	—	—	—	—	—	—	+† (occas.)	—	+
Wrightia	5	20-30	+	80-110	1, 2-3	+	—	—	+	—	+	+	—	—	—	+	—

* Containing elongated crystals.

† Reported to be present, not observed in material examined.

in two genera with irregularly spaced bands there is also paratracheal parenchyma (*Cerbera* and *Cerberiopsis*).

(*f*) Long radial multiples of vessels characteristic of many genera.

(*g*) Latex tubes observed in the rays of two genera and reported in two others.

(*h*) Latex traces observed in seven of the genera and reported in others.

Anatomically the family may be readily divided into two groups on the presence or absence of septate fibres and the abundance and distribution of parenchyma. The group characterized by septate fibres—*Ervatamia*, *Rejoua*, and *Voacanga*—(of those examined) has poorly developed parenchyma, either sparse paratracheal or entirely lacking; this group is also marked by the presence of distended cells somewhat resembling oil cells, never abundant but scattered through the marginal upright cells of the rays. The other genera have non-septate fibres with small, but generally distinctly bordered, pits; the parenchyma is not uniform, varying from apotracheal bands and diffuse, together with some paratracheal, generally incompletely vasicentric in *Cerbera* and *Cerberiopsis* to entirely apotracheal, either diffuse to reticulate or in bands, in the remainder.

This subdivision of the genera on anatomical features bears little or no relation to the botanical classification of the family after K. Schuman in Engler and Prantl (1889). However, the three genera, *Ervatamia*, *Rejoua*, and *Voacanga* referred to above as making one group anatomically are all classified together by Schuman in the subgroup Tabernaemontaninae of the Plumeriae in which most of the genera under discussion are classed. An artificial key to the 12 genera studied, based on anatomical features only, is set out below:

Artificial key to grouping of 12 *genera of the Apocynaceae occurring in the south-west Pacific area*

1. Fibres non-septate, pits numerous and generally distinctly bordered
    - *A.* Parenchyma paratracheal and in irregularly spaced bands; vessels characteristically in long radial multiples up to 8 or more . . . . *Cerbera*, *Cerberiopsis*
    - *B.* parenchyma apotracheal, in regularly to irregularly spaced bands 1-3 cells wide; latex tubes present in rays . . . . *Alstonia I*
    - *C.* Parenchyma in fine, short, uniseriate lines, latex tubes present in rays . . . . . . *Dyera*
    - *D.* Parenchyma mainly diffuse with tendency to form short reticulate lines between rays, latex tubes absent from rays
        - (*a*) Vessels predominantly in radial multiples up to 6, occasionally 8 or more
            - (1) Rays weakly heterogeneous . . . . *Alstonia II*
            - (2) Rays markedly heterogeneous . . . . *Wrightia*, *Kibatalia*, *Vallaris*
        - (*b*) Vessels predominantly to exclusively solitary . . . . *Hunteria*, *Ochrosia*
2. Fibres septate; pits inconspicuous, simple; parenchyma sparse paratracheal to absent . . . . *Voacanga*, *Ervatamia*, *Rejoua*

Metcalfe and Chalk (1950) have noted a similarity between the woods of group 2 (see key above) and a group of woods of the Euphorbiaceae which they refer to as the Phyllanthoideae group B '*Glochidion*' type. These woods also show septate fibres and a general lack of parenchyma (with one or two exceptions). However, there are several important differences. With the exception of *Bridelia* and *Cleistanthus* the vessel pitting, though small and generally comparable, is not vestured; the pitting between vessels and ray cells is half-bordered, almost simple, elongated, and often scalariform (minute, circular ray-vessel pitting in *Cleistanthus*); the rays, although heterogeneous and often of two widths, are in the main composed of central cells which are short, sometimes square to brick-shaped, contrasting little with the marginal upright cells and cells of the uniseriate rays; whereas in group 2 of the Apocynaceae, and also in some genera of group 1, there is marked contrast in dimension. Some woods of the Euphorbiaceae do possess latex tubes and channels similar to the latex traces found in the Apocynaceae but these seem to be confined to the Section Crotonoideae.

There are, however, several genera of the Rubiaceae that could be confused anatomically with group 2 of the Apocynaceae. Features common to both are septate fibres, sparse parenchyma, long radial multiples of small pores, vestured pits, ray-vessel pitting similar to inter-vessel type (frequently also unilaterally compound in the two families), and similarity in ray type in many instances, the rays being extremely heterogeneous with a tendency to two distinct widths, the upright cells being disjunctive. Examples of these genera are *Alseis, Calycophyllum, Hamelia,* and *Mastixiodendron.*

(B) ANNONACEAE

I. General

In this family there are some 80 genera of climbers, shrubs, and small to medium-sized trees, but few genera produce species of commercial importance from a timber standpoint. Record and Hess (1943) have referred to 21 genera occurring in tropical America and Hess (1946) has described the anatomy of the timbers of these genera.

One genus, *Oxandra,* is of commercial importance in the New World; *O. lanceolata* (Sw.) Baill. produces the lancewood of commerce, a timber used for shafts, tool handles, archers' bows, etc.

Metcalfe and Chalk (1950) have summarized the anatomical features of the family as a whole; in the present discussion 12 genera occurring in the south-west Pacific area have been treated more specifically and methods for their identification discussed.

A few genera are said to be used locally to a limited extent; these include *Cyathocalyx* in the Philippines (Reyes 1928), *Mezzettia* in Malaya (Desch 1941), and *Xylopia* in both Malaya and the Philippines. Some members of the family have been identified in shipments of timber reaching the Australian market. Mention has been made in the literature of the absence of sharply defined heartwood in the family; Hess (1946) states that heartwood, distinctive in colour from sapwood, is formed only in larger trees or in association with wounds or knots. Desch (1941) records that in the examination of timbers from 11 genera sapwood and heartwood were not clearly differentiated and that only in one species of *Polyalthia* was there a small central core of wood darker in colour and sharply differentiated from that further out. He also mentions the abundance of starch in the woods of this family. Thus it seems probable that there is little heartwood formation.

The distribution in the south-west Pacific area of the genera examined is shown in Figure 2.

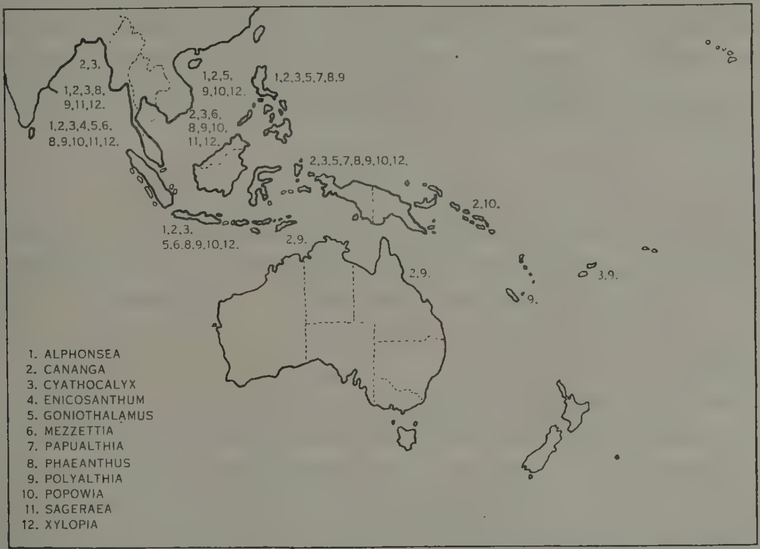

2,3.
1,2,3,8.
9,11,12.
1,2,3,4,5,6.
8,9,10,11,12.
1,2,5.
9,10,12.
1,2,3,5,7,8,9
2,3,6.
8,9,10.
11,12.
2,3,5,7,8,9,10,12.
2,10.
1,2,3.
5,6,8,9,10,12.
2,9.
2,9.
3,9.
9.
1. ALPHONSEA
2. CANANGA
3. CYATHOCALYX
4. ENICOSANTHUM
5. GONIOTHALAMUS
6. MEZZETTIA
7. PAPUALTHIA
8. PHAEANTHUS
9. POLYALTHIA
10. POPOWIA
11. SAGERAEA
12. XYLOPIA

Fig. 2.—Distribution of genera of Annonaceae examined from the south-west Pacific.

II. ANATOMICAL CHARACTERISTICS OF THE GENERA EXAMINED

The procedure adopted in studying the anatomy of the various genera was the same as for the Apocynaceae and results obtained have been set out in Table 3.

(*a*) *Alphonsea*

(i) *General.*—A genus of some 12 species of shrubs and small to medium-sized trees occurring from north-eastern India to southern China and Malaysia. *A. arborea* (Blanco) Merr. of the Philippines (Reyes 1938) is said to be a moderately dense and strong timber of some commercial importance for general construction, and, owing to its toughness, for tool handles and agricultural implements; only one unassigned species from Malaya was available for examination; this is a pale brown to greyish brown timber, moderately heavy and fissile.

(ii) *Structure.*—*Growth rings* indistinctly marked by bands of somewhat denser fibres. *Vessels* evenly distributed, moderately small and indistinct to the naked eye; maximum tangential diameter 117 μ; mean member length 530 μ; numerous (11-12/sq. mm.); solitary (40 per cent.) and in radial multiples up to four, with a few small clusters; perforation plates simple, oblique; inter-vessel pitting very small, bordered, alternate, diameter of borders 4-6 μ. *Rays* few (3-4/mm.), majority 2-4-seriate, and moderately high, up to 60 cells; weakly heterogeneous with one row of squarish cells at margins; uniseriate to partly biseriate rays very few and low, up to 6 or 8 cells; vessel-ray pitting half-bordered and similar in appearance to inter-vessel pitting; yellow oil deposits observed in unspecialized cells. *Parenchyma* apotracheal, in fine bands 1 or 2 cells wide spaced 3-6 fibres apart, in more or less regular arrangement, interrupted by the rays; oil cells not observed. *Fibres* moderately thick-walled, nonseptate with numerous, small, indistinctly bordered pits; mean length 1.27 mm.

(iii) *Material.—Alphonsea* sp. (unassigned), one sample Malaya.

(*b*) *Cananga*

(i) *General.*—A genus of three species of trees or shrubs occuring from Burma and Malaysia to Australia. *C. odorata* has the widest distribution, being found in Malaya, the Philippines, New Guinea, the Solomon Is., and Australia; in addition, the species is frequently cultivated for its flowers. The timbers are generally fairly coarse-textured, of a pale colour, light, and soft, and prone to fungal attack.

(ii) *Structure.—Growth rings* generally inconspicuous. *Vessels* visible to distinct to the naked eye; maximum tangential diameter 260 μ; mean member length 360-790 μ; few (1-3/sq. mm.) and evenly distributed; up to 50 per cent. solitary, the remainder in radial multiples of 2 or 3, occasionally up to 4; perforation plates simple; inter-vessel pitting moderately coarse, bordered alternate, diameter of borders 10-13 μ (Plate 7, Fig. 3). *Rays* generally few (2-3/mm.), 3-9-seriate, high, sometimes of over 100 cells, homogeneous to weakly heterogeneous with one row of squarish cells (Plate 8, Fig. 3); uniseriate to partly biseriate rays few and low, generally 2-6 cells high; vessel-ray pitting half-bordered and similar to inter-vessel pitting; oil cells not observed though stated to be present (Janssonius 1908). *Parenchyma* apotracheal in fine uniseriate to partly biseriate lines, spaced 4-6 fibres apart, and some paratracheal to vasicentric; oil cells sporadic in different samples. *Fibres* thin-walled, nonseptate, with numerous indistinctly bordered pits on radial and tangential walls; mean length 0.83-1.87 mm.

(iii) *Material.—Cananga odorata* (Lamk.) Hook.f. et Thoms., six samples New Guinea and Solomon Is.; *C.* sp. (unassigned) one sample Ceylon.

(*c*) *Cyathocalyx*

(i) *General.*—A genus of small to medium-sized trees occurring from Ceylon to Burma through Malaysia to New Guinea. The timbers vary in density and properties, the Malayan species *C. maingayi* being a light yellow-brown with a pale greenish tinge and moderately light in weight; and the Philippine, *C. globosus,* stated to be a reddish brown, dense, and strong timber (Reyes 1938).

(ii) *Structure.—Growth rings* generally marked by a narrow band of denser fibres. *Vessels* visible to the naked eye; maximum tangential diameters 205-250 μ; mean member length 660-840 μ; evenly distributed, numbering 2-3/sq. mm., between 40 and 60 per cent. solitary, remainder in radial multiples of 2 or 3, sometimes up to 4, several clusters (Plate 7, Fig. 2); perforation plates simple; inter-vessel pitting fine, bordered, alternate, the borders 4-6 μ in diameter. *Rays* few (2-3/mm.) generally 3-6-seriate, occasionally biseriate; extremely high, sometimes over 100 cells, practically homogeneous to weakly heterogeneous with one row of squarish marginal cells; uniseriate rays infrequent and generally low, 6-10 cells; vessel-ray pitting half-bordered and similar to inter-vessel pitting; oil cells, usually solitary, observed in all samples (Plate 9, Fig. 4). *Parenchyma* apotracheal bands 1 or 2 cells wide, extremely regular and spaced 3 or 4 fibres apart; paratracheal parenchyma present (Plate 8, Fig. 1), incompletely vasicentric to sparse; oil cells observed in all samples, tending to be adjacent to the rays (Plate 9, Fig. 1). *Fibres* non-septate, moderately thin-walled; pits numerous and indistinctly bordered; mean length 1.28-1.66 mm.

(iii) *Material.—Cyathocalyx maingayi* Hook.f., one sample Malaya; *C. polycarpum* White and Francis, three samples New Guinea; *C.* sp. nov., two samples New Guinea.

(*d*) *Enicosanthum*

(i) *General.*—A monotypic genus occurring in Borneo and Malaya. *E. fuscum* is a small tree of the lowland dipterocarp forests (Desch 1941). The only sample available is pale yellow-brown, moderately light and soft, and straight-grained; texture medium; apparently of no commercial importance.

(ii) *Structure.—Growth rings* indistinctly indicated by slight thickening of fibre walls. *Vessels* visible to the naked eye; maximum tangential diameter 190 μ; mean member length 560 μ; few to moderately numerous (4-7/sq. mm.), evenly distributed; solitary (60 per cent.) and in radial multiples of 2 or 3, with occasional small clusters; perforation plates simple; inter-vessel pitting very small, bordered, alternate, diameter of borders 4-5 μ. *Rays* few (3-4/mm.), 5-10-seriate; high, up to 90 cells; uniseriate to partly biseriate rays few and very low, 3-7 cells; homogeneous to weakly heterogeneous with one row of squarish cells at margins, particularly in uniseriate rays; vessel-ray pitting small, half-bordered, and similar to inter-vessel pitting; oil cells not observed; deposits of extraneous material sporadic. *Parenchyma* apotracheal in fine lines 1 or 2 cells wide, numerous, in regular arrangement 3-5 fibres apart interrupted by the rays; oil cells not observed. *Fibres* moderately thick-walled, non-septate with numerous small, indistinctly bordered pits; mean length 1.35 mm.

(iii) *Material.—Enicosanthum fuscum* (King) Airy-Shaw, one sample Malaya.

(*e*) *Goniothalamus*

(i) *General.*—A large genus of shrubs and small trees occurring throughout tropical Asia. A single sample of one species, *G. grandiflorus* (Warb.) Boerl., was available for examination. The wood is very light and soft and of a pale straw colour.

(ii) *Structure.—Growth rings* not evident. *Vessels* evenly distributed, moderately small and indistinct to the naked eye; maximum tangential diameter 145 μ; mean member length 568 μ; moderately numerous (5-10/sq. mm.); solitary (45 per cent.) and in radial multiples up to 4; perforation plates simple, oblique; inter-vessel pitting small, bordered, alternate, diameter of borders 4-6 μ. *Rays* few (2-3/mm.); majority 3-6-seriate and high, up to 140 cells, 2-3/mm., composed almost entirely of procumbent cells; uniseriate to partly biseriate rays few and generally less than 10 cells high; vessel-ray pitting similar to the inter-vessel pitting; small crystals always present, usually one per cell (Plate 7, Fig. 5). *Parenchyma* apotracheal in fine bands 1 or 2 cells wide, spaced 3-6 fibres apart more or less regularly, interrupted by the rays; oil cells and crystals not observed. *Fibres* thin-walled, non-septate, with numerous small, indistinctly bordered pits; mean length 1.12 mm.

(iii) *Material.—Goniothalamus grandiflorus* (Warb.) Boerl., one sample, New Guinea.

(*f*) *Mezzettia*

(i) *General.*—A genus of trees occurring in the Indo-Malayan region. *M. leptopoda* Oliv. is said to be a medium to large tree (Desch 1941); the wood is pinkish to yellowish brown with streaks of grey, moderately dense, and straight-grained.

(ii) *Structure.—Growth rings* indistinct. *Vessels* evenly distributed, distinct to the naked eye; maximum tangential diameter 175-245 μ; mean member length 600-700 μ; few to moderately numerous (2-5/sq. mm.); solitary (26-40 per cent.) and in radial multiples of 2-6; perforation plates simple; inter-vessel pitting moderately fine, bordered, alternate, diameter of borders 9-10 μ. *Rays* few (2-3/mm.) mainly 4-8 cells wide; high, over 100 cells; homogeneous to weakly heterogeneous, uniseriate rays few and low, up to 10 cells; procumbent ray cells somewhat variable in vertical dimension; vessel-ray pitting half-bordered and similar to inter-vessel pitting; no silica or crystals observed; oil or mucilage cells reported by Metcalfe and Chalk (1950) but none observed in material examined. *Parenchyma* apotracheal in fine, 1- to sometimes 2-celled bands, closely spaced, varying from 2 to 4 fibres apart. *Fibres* moderately thick-walled, non-septate, pits indistinctly bordered; mean length 1.20-1.36 mm.

(iii) *Material.—Mezzettia leptopoda* Oliv., one sample, Malaya; *M.* sp. (unassigned), one sample, Malaya.

(*g*) *Papualthia*

Two unassigned samples representing this genus were originally considered under *Polyalthia.* They are both light and soft, and brownish grey in colour. The only anatomical feature that distinguishes these two samples from *Polyalthia* is the regular presence of small crystals, usually only one per cell, in the ray cells and occasionally also in the vertical parenchyma. The presence of crystals has not been noted in any other genus of this family examined in this work, except *Goniothalamus,* in which genus *Polyalthia* was once included.

(*h*) *Phaeanthus*

(i) *General.*—A genus of small trees found through the Indo-Malayan region to New Guinea; one species was available for examination, the wood of which is pale yellow, moderately heavy, and straight-grained.

(ii) *Structure—Growth rings* indistinct. Vessels indistinct to the naked eye; maximum tangential diameter 153 μ; mean member length 510 μ; moderately numerous (5-6/mm.); evenly distributed; solitary (47 per cent.), remainder in radial multiples of 2 or 3, occasionally up to 4; perforation plates simple; inter-vessel pitting minute, bordered, alternate, diameter of borders 2-3 μ. *Rays* 1-5-seriate, maximum height up to 70 cells; uniseriate rays generally very low, less than 10 cells; weakly heterogeneous with 1 or 2 rows of squarish cells at margins; vessel-ray pitting minute (Plate 7, Fig. 4); half-bordered, and similar to inter-vessel pitting; oil cells not observed. *Parenchyma* apotracheal in fine bands mainly 1 cell wide, spaced 3-7 fibres apart; oil cells not observed. *Fibres* non-septate, moderately thick to thick-walled with numerous fine, indistinctly bordered pits; mean length 1.36 mm.

(iii) *Material.—Phaeanthus macropodus* (Miq.) Diels, one sample, Malaya.

(*i*) *Polyalthia*

(i) *General.*—A rather large genus of shrubs and trees with a wide distribution from tropical Africa, Madagascar, through tropical Asia, Malaysia, Australia, and New Guinea; eight species from New Guinea, Malaya, Borneo, and northern Australia were available for examination; the woods of these species are generally pale brown, pinkish, or yellowish brown, sometimes quite yellow, moderately heavy, straight-grained, and generally fine-textured, the rays being a prominent feature of the quarter section, varying in height from 1 to 5 mm.

(ii) *Structure.—Growth rings* indistinct to sometimes well marked with slightly thicker-walled fibres in the late wood. *Vessels* indistinct to distinct to the naked eye; maximum tangential diameters varying from 120 to 220 μ; mean member length 440-660 μ; moderately numerous (5-12/sq. mm.), solitary (25-45 per cent.) and in radial multiples up to 4; perforation plates exclusively simple; inter-vessel pitting very small to minute, bordered, alternate, the borders 2-4 μ in diameter. *Rays* 3-9-seriate, sometimes up to 10 cells wide, over 100 cells high; homogeneous to weakly heterogeneous; in most species, however, horizontal series of brick-shaped to erect cells occur, as seen on radial sections, among the procumbent rows (Plate 9, Fig. 3); as a result of this the cells vary greatly in size as seen on tangential section (Plate 8, Fig. 4); uniseriate to partly biseriate often infrequent, but quite numerous in one species (*P. holtzeana*); very low, up to 10 cells; vessel-ray pitting half-bordered, similar to the inter-vessel pitting; deposits of extraneous material are sometimes present; crystals sparse in some samples of *P. holtzeana*; oil cells not observed. *Parenchyma* apotracheal in fine bands 1 or 2 cells wide, spaced 3-8 fibres apart; oil cells were observed in one species (*P. oblongifolia* Burck.) (Plate 9, Fig. 2). *Fibres* non-septate, moderately thick-walled, with indistinctly bordered pits, mean length 1.18-1.56 mm.

(iii) *Material.—Polyalthia canangioides* Boerl., one sample Malaya; *P. cinnamomea* Hook.f., one sample Malaya; *P. discolor* Diels, two samples New Guinea; *P. holtzeana* F.Muell., five samples north Australia; *P. hypoleuca* Hook.f. et Thoms., two samples Malaya; *P. jenkensii* Hook.f., one sample North Borneo; *P. oblongifolia* Burck., two samples New Guinea; *P.* sp. nov., two samples New Guinea.

(*j*) *Popowia*

(i) *General.*—A genus of some 25 species of shrubs and small trees from the Indo-Malayan region; only one sample of an unassigned species was available for examination. The wood of this sample is pale yellowish to greyish brown, moderately light, and straight-grained; the rays are conspicuous on all faces.

(ii) *Structure.—Growth rings* marked fairly distinctly by thicker-walled fibres in the late wood. *Vessels* small and indistinct to the naked eye; maximum tangential diameter 145 μ; mean member length 440 μ; moderately numerous (7-8/sq. mm.), rather variable in size, evenly distributed, 40 per cent. solitary, the remainder in radial multiples of 2 or 3; perforation plates simple; inter-vessel pitting minute, bordered, alternate; the diameter of the borders 3-4 μ. *Rays* mainly 3-12 cells wide with a preponderance of rays 6-10-seriate; extremely high, over 100 cells; few (1-3/mm.); homogeneous to weakly heterogeneous; uniseriate to partly biseriate few and generally less than 10 cells high; vessel-ray pitting half-bordered and similar to inter-vessel pitting; oil cells not observed. *Parenchyma* apotracheal in regular, fine bands looped between the rays, 1 to sometimes 2 cells wide in part, spaced 4-6 fibres apart; oil cells not observed. *Fibres* moderately thin-walled with indistinctly bordered pits; mean length 1.25 mm.

(iii) *Material.—Popowia* sp. (unassigned), one sample, New Guinea.

(*k*) *Sageraea*

(i) *General.*—A genus of six or eight species of small trees. *S. elliptica* Hook.f. et Thoms., Andaman bow-wood, from the Andamans and Tenasserim, is of some commercial importance locally; Pearson and Brown (1932) have described the anatomy of this species. *S. lanceolata*, the only species available for examination, occurs in Borneo and Malaya; the sample available, unlike *S. elliptica*, is moderately light and soft and medium in texture, whereas *S. elliptica* is described by the above authors as a hard, heavy, fine-textured wood that is tough and elastic; Desch (1941) also describes a single sample of *S. lanceolata* as having a density of over 45 lb./cu. ft.

(ii) *Structure.—Growth rings* sometimes distinctly marked by a thin band of denser fibres and a somewhat closer spacing of the fine bands of parenchyma. *Vessels* mainly indistinct to the naked eye; maximum tangential diameter 158 μ; mean member length 690 μ; few (3-4/sq. mm.); evenly distributed; solitary (52 per cent.) and in radial multiples of 2-4, clusters fairly common; perforation plates simple; inter-vessel pitting minute; bordered, alternate, diameter of borders 3-4 μ. *Rays* up to 9-seriate, mainly 4-7; few (4-5/mm.); up to 70 cells high; uniseriate to partly biseriate rays few, generally very low, less than 10 cells; weakly heterogeneous with one or two rows of squarish marginal cells; cells on tangential section very diverse in size, the larger cells appearing in radial section as horizontal series of squarish cells; vessel-ray pitting half-bordered and similar to inter-vessel pitting; fine crystals present, sparse; no oil cells observed. *Parenchyma* apotracheal in fine regular bands 1 or 2 cells wide, spaced 4-6 fibres apart, generally more closely spaced in the late wood; sometimes disjunctive; oil cells not observed. *Fibres* moderately thin-walled, non-septate, pits indistinctly bordered and small; mean length 1.22 mm.

(iii) *Material.—Sageraea lanceolata* Miq., one sample, Borneo.

(*l*) *Xylopia*

(i) *General.*—A large genus of some 60 species of shrubs and generally small trees widely distributed in the tropics of the New World and the Malaysian and Asiatic regions and Africa; five species were available for examination. Few species are of commercial importance, *X. fusca* Maing. ex Hook.f. and *X. caudata* Hook.f. are reported to be used to a small extent in Malaya (Desch 1941). The timbers vary considerably from light and soft to moderately dense and hard, medium to coarse-textured, straight-grained, colour yellowish to greyish brown; rays conspicuous on all faces.

(ii) *Structure.—Growth rings* sometimes distinct, with a narrow band of distinctly thicker-walled fibres. *Vessels* intermediate in size and indistinct to the naked eye, to large and distinct to the naked eye (*X. fusca*); maximum tangential diameters 165-325 μ; mean member length 490-750 μ; perforation plates simple; inter-vessel pitting small, moderately coarse, bordered, alternate, diameter of borders varying from 6 to 9 μ in all species except *X. fusca* (9-12 μ). *Rays* very varied; in three species examined (*X. dehiscens* (Blanco) Merr., *X. tremblingensis* Hend., and *X.* sp. (unassigned)) 1-4-seriate, majority 2 or 3 cells wide, practically homogeneous up to 80 cells high, ray cells generally thick-walled (Plate 8, Fig. 5); remainder of species with rays generally 3-8 cells wide, uniseriate rays few and generally very low, ray cells typically thin-walled and similar to other genera examined; horizontal series of enlarged cells observed in *X. papuana*; vessel-ray pitting half-bordered and similar to inter-vessel pitting; oil cells not observed. *Parenchyma* apotracheal, in fine bands 1 or 2 cells wide spaced 4-6 fibres apart; in the three species with thick-walled ray cells, the vertical parenchyma cells are also thick-walled; sometimes disjunctive; no oil cells observed. *Fibres* non-septate; medium to thick-walled, pits indistinctly bordered; mean length 1.2-1.5 mm.

(iii) *Material.—Xylopia calosericea* Diels, one sample New Guinea; *X. dehiscens* (Blanco) Merr., one sample Sarawak; *X. ferruginea* Hook.f. et Thoms. var. *oxantha* J. Sinclair, one sample Borneo; *X. fusca* Maing. ex Hook.f., two samples Malaya. *X. papuana* Diels, five samples New Guinea and Solomon Is.; *X. tremblingensis* Hend., one sample Malaya; *X.* sp. unassigned, two samples New Guinea; *X.* sp. aff. *papuana*, one sample New Guinea.

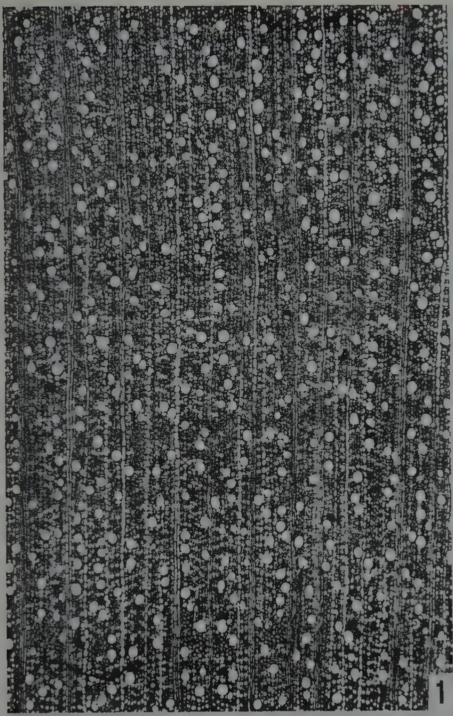
TABLE 3

SUMMARY OF ANATOMICAL CHARACTERISTICS OF 10 GENERA OF THE ANNONACEAE OCCURRING IN THE SOUTH-WEST PACIFIC AREA

Genera Examined	Pores				Rays			Parenchyma			Fibres
	Percentage Solitary	Maximum Tangential Diameter (μ)	Vessel Member Length (μ)	Diameter of Pit Borders (μ)	Predominant Widths (No. of cells)	Oil Cells (sol.)	Radial Series of Enlarged (cells)	Para-tracheal Present	Width of Apotra-cheal Bands (cells)	Oil Cells (sol.)	Fibre Length (mm.)
Alphonsea	40	117	530	4-6	(1), 2-4	—[2]	—	—	1-2	—[2]	1·27
Cananga	50	240-260	360-790	10-13	(1), 3-9	—	—	+	1-2	+	0·83-1·87
Cyathocalyx	40-60	205-250	660-840	4-6	(1), 3-7	+	—	±	1-2	±	1·28-1·66
Enicosanthum	60	190	560	4-5	(1), 4-10	—	—	—	1-2	—	1·35
Goniothalamus . .	45	145	570	4-6	(1), 3-6	—	—	—	1-2	—	1·12
Mezzettia	26-40	175-245	600-700	9-10	(1), 4-8	+	+	+	1-(2)	—	1·20-1·36
Phaeanthus	47	153	510	2-3	1-5	—	—	—	1-(2)	—	1·36
Polyalthia	25-45	120-220	440-660	2-4	(1), 3-10	—	+[3]	—	1-(2)	—[5]	1·18-1·56
Popowia	40	145	440	3-4	(1), 3-10	—	—	—	1-2	—	1·25
Sageraea	52	158	690	3-4	(1), 3-9	—	+	—	1-2	—	1·22
Xylopia	23-60	165-325	490-750	6-9	(1), 2-8	—	—[4]	—	1-(2)	—	1·20-1·50
				(9-12)[1]	1-4						

1. *X. fusca.*
2. Oil present in unspecialized cells, both ray and vertical parenchyma.
3. Present in all species but *P. canangioides* and one unassigned species.
4. Absent in all species but *X. papuana.*
5. Absent in all but one unassigned species.

WOOD ANATOMY OF APOCYNACEAE AND ANNONACEAE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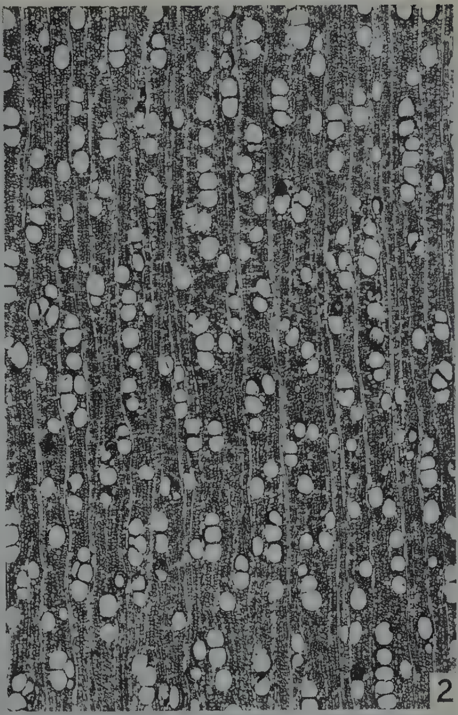
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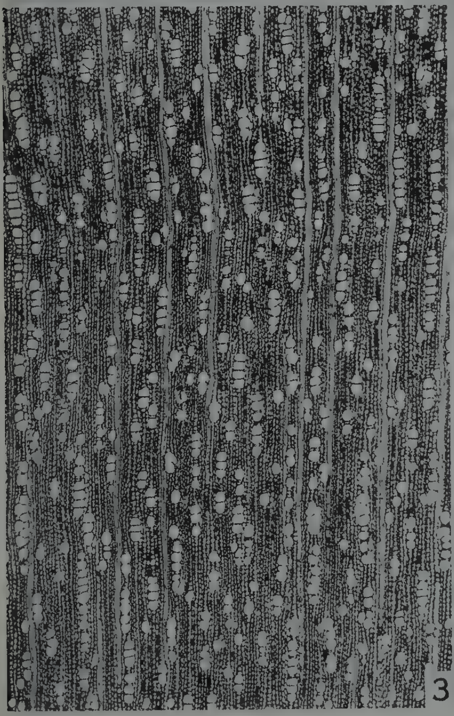
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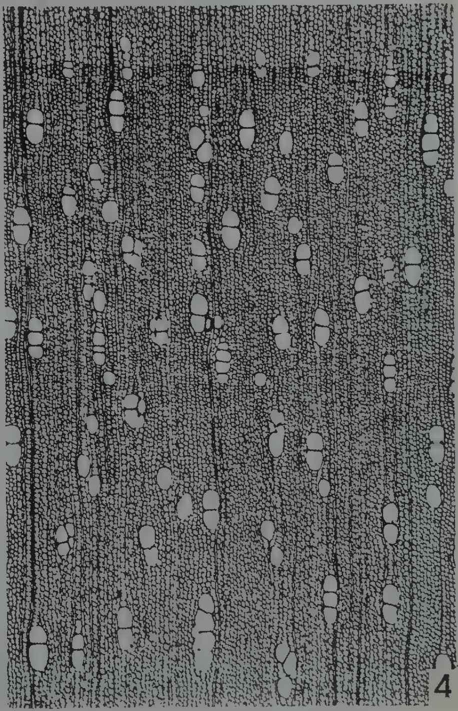
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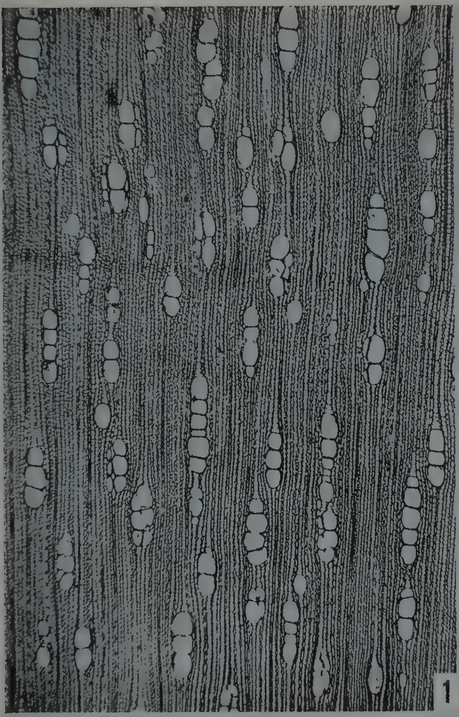

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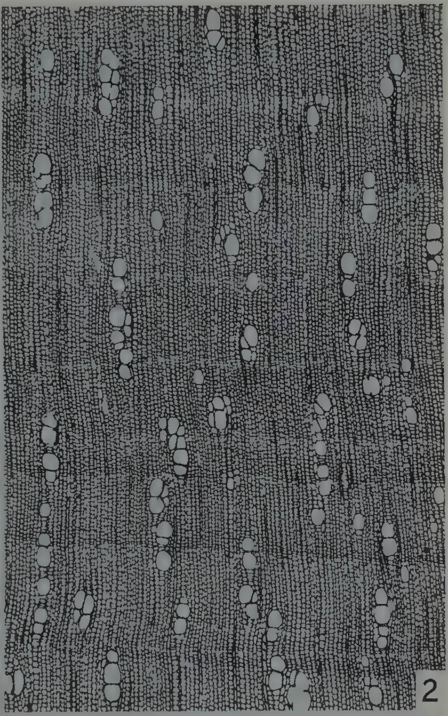

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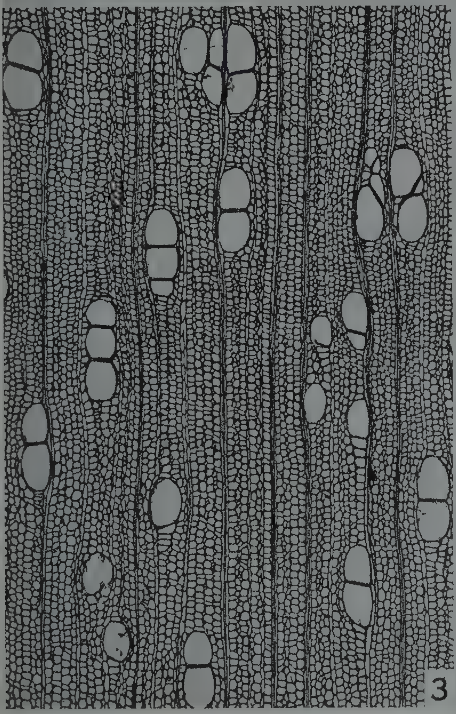

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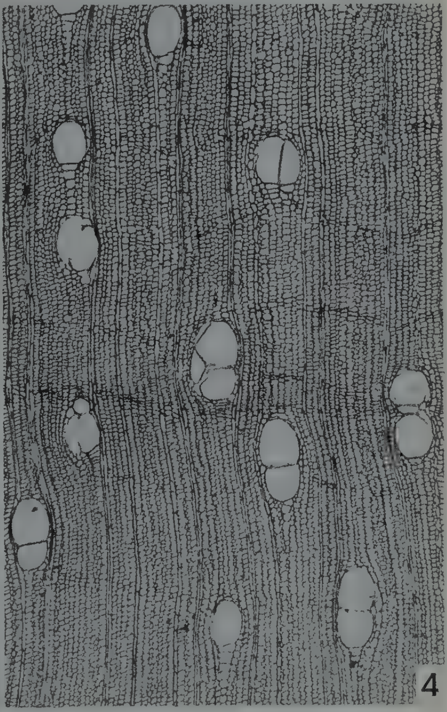

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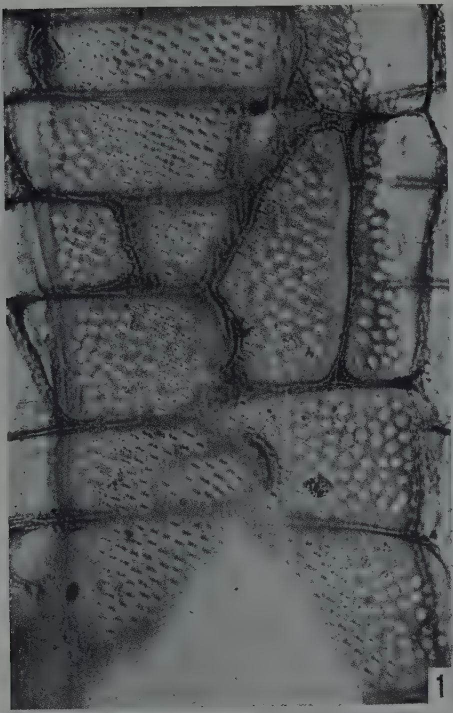

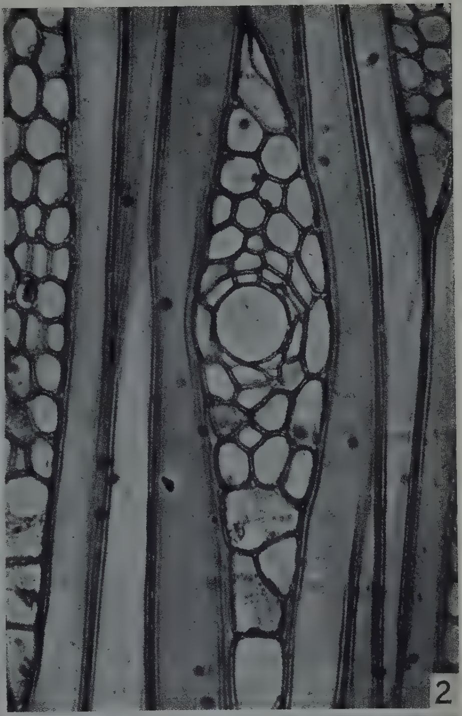

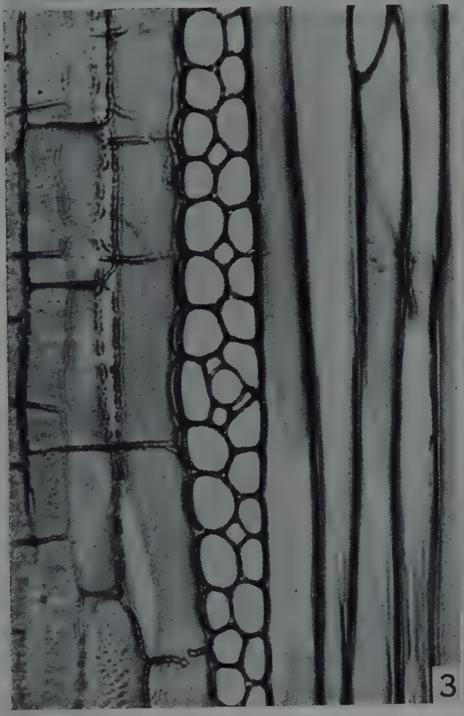

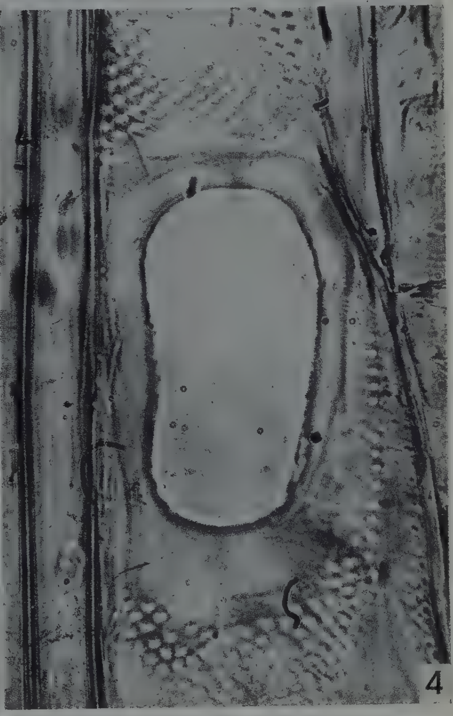

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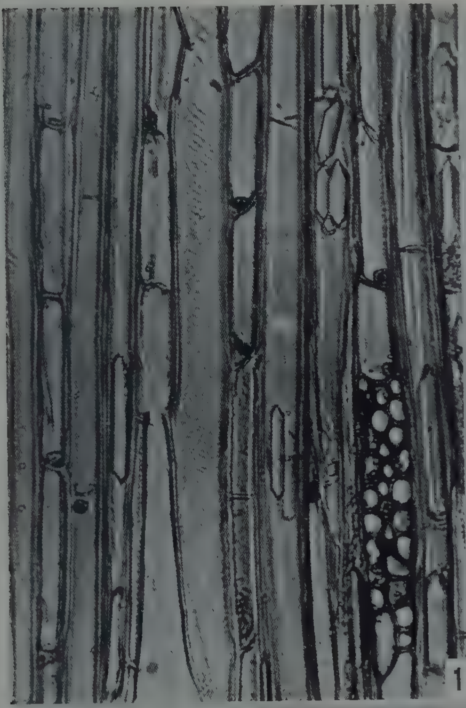

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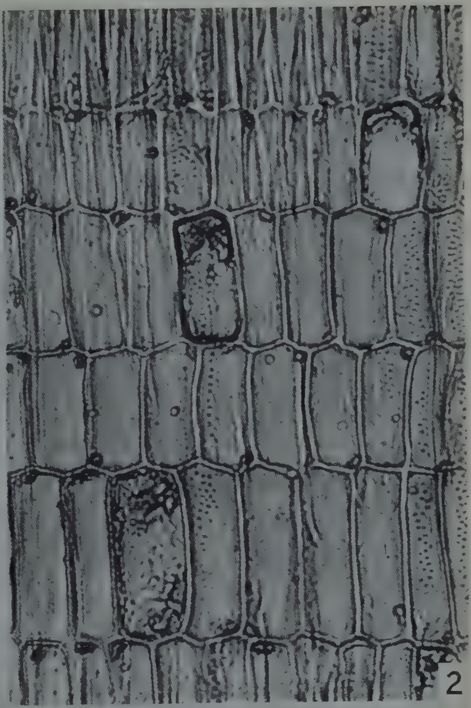

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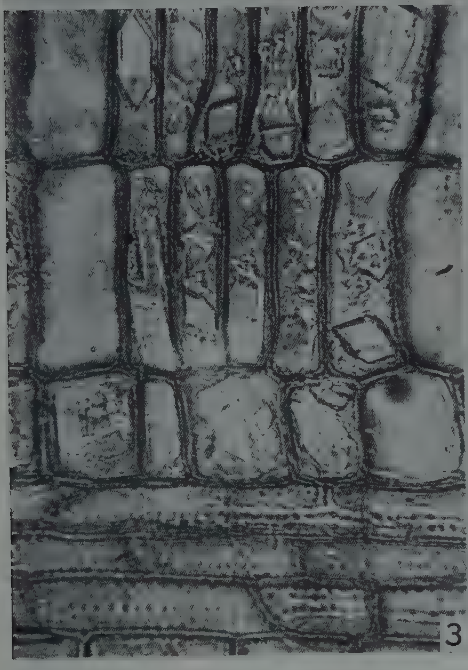

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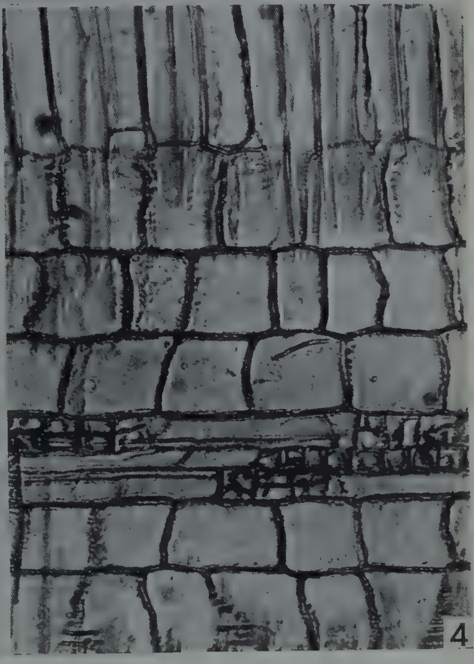

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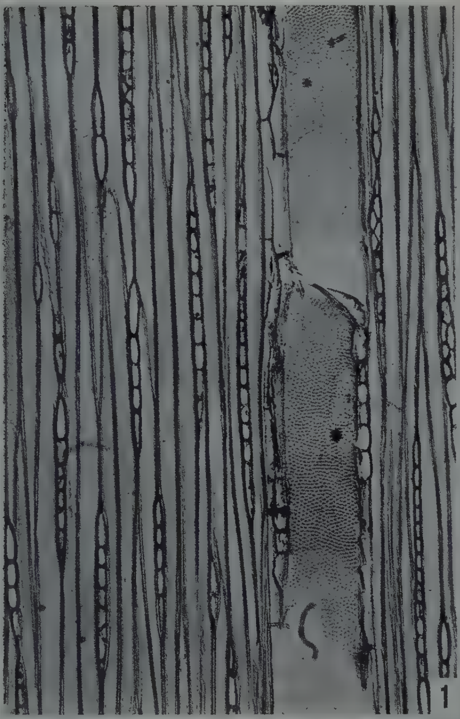
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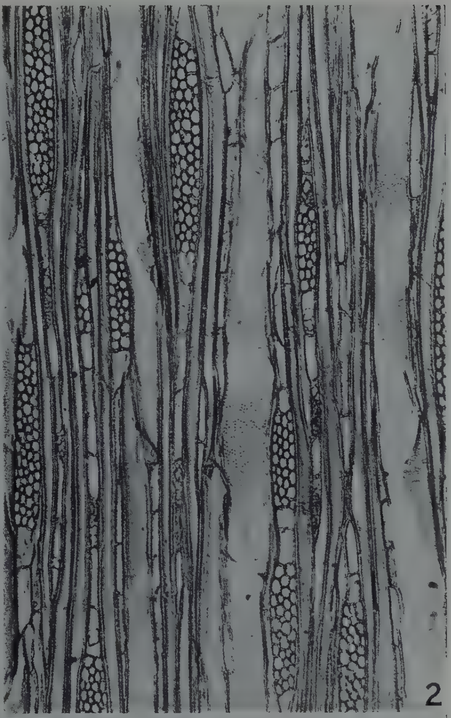
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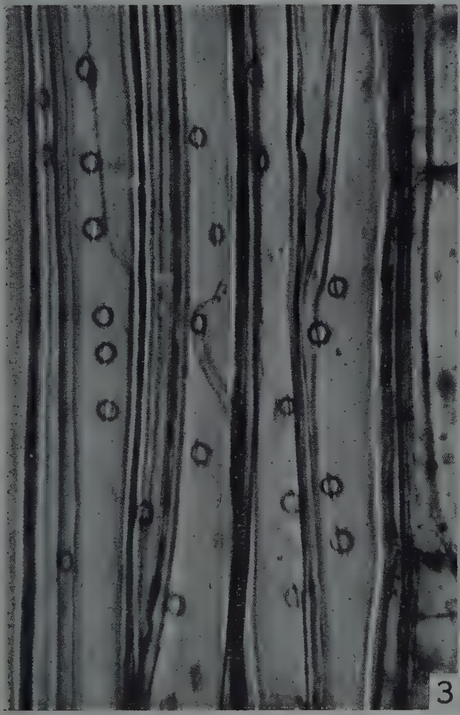
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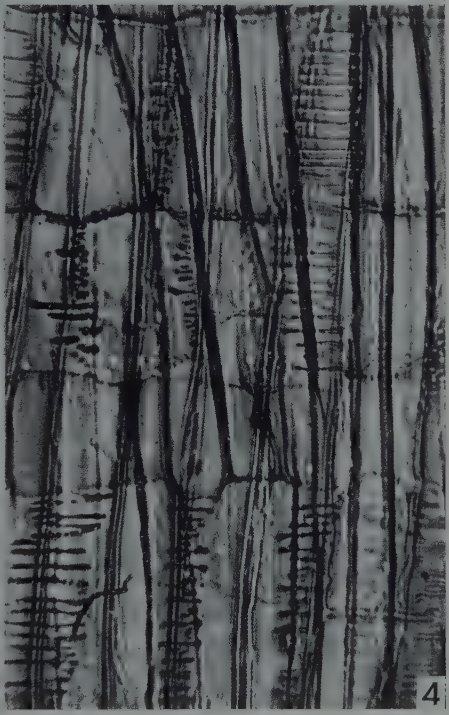
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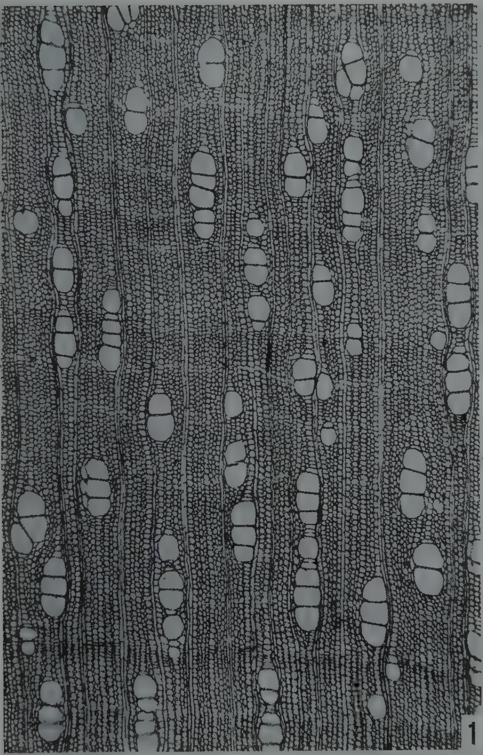
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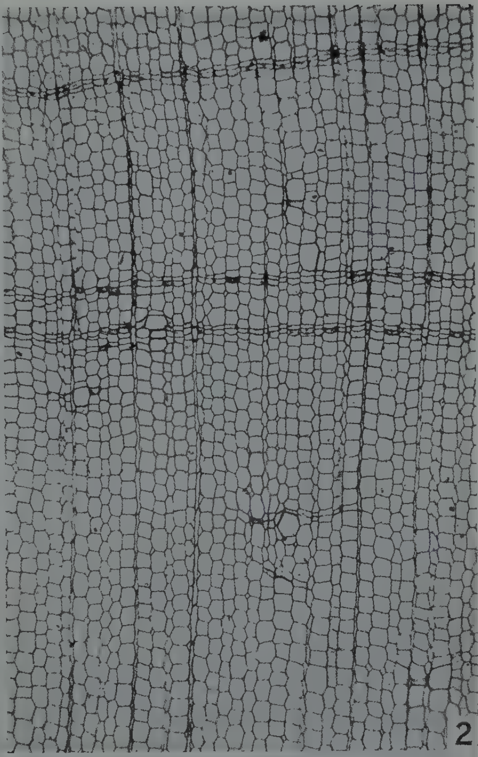
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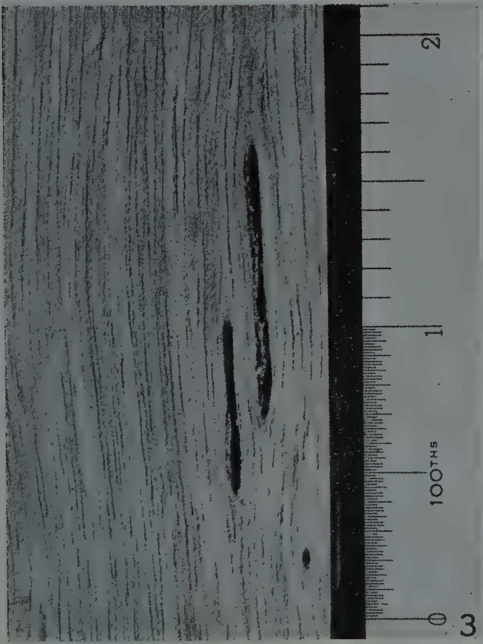

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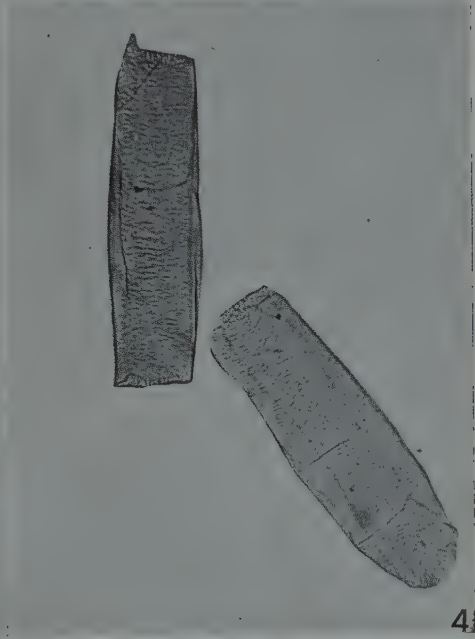
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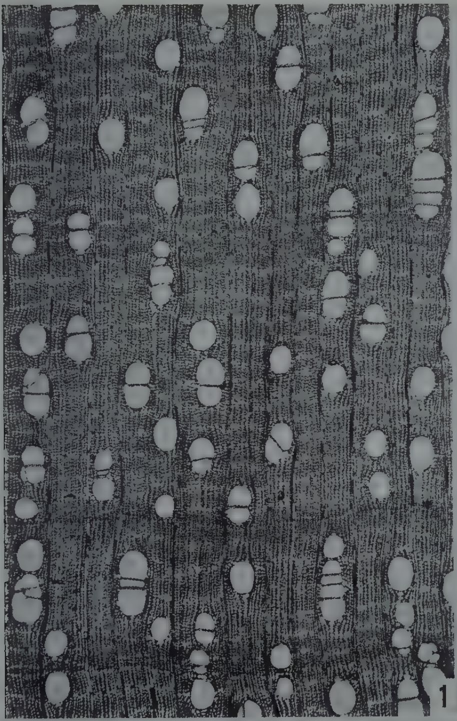

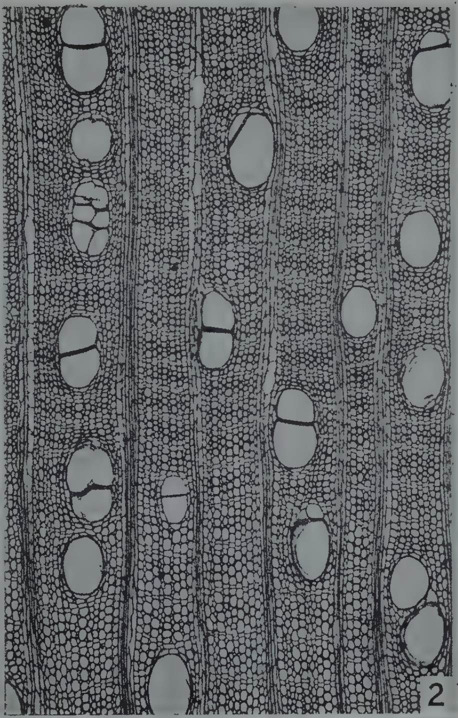

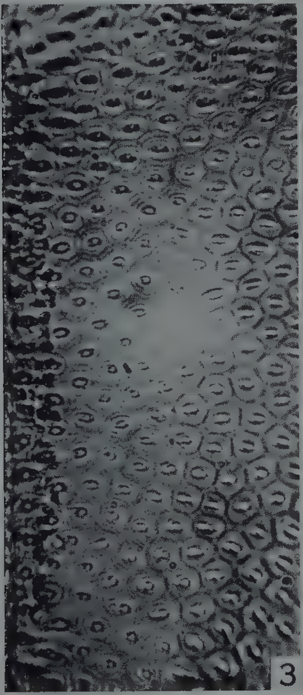

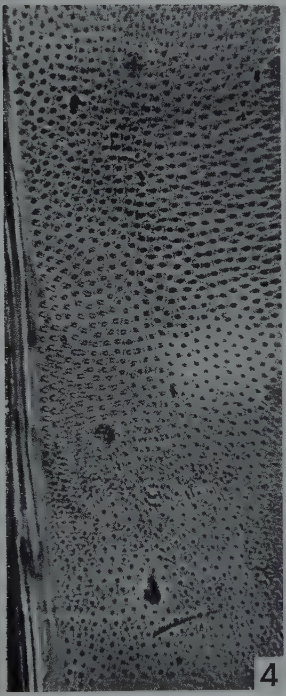

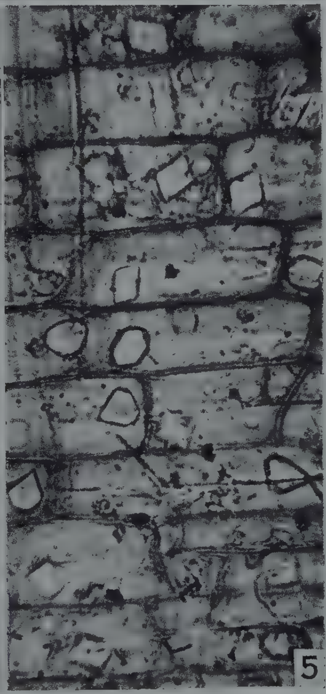

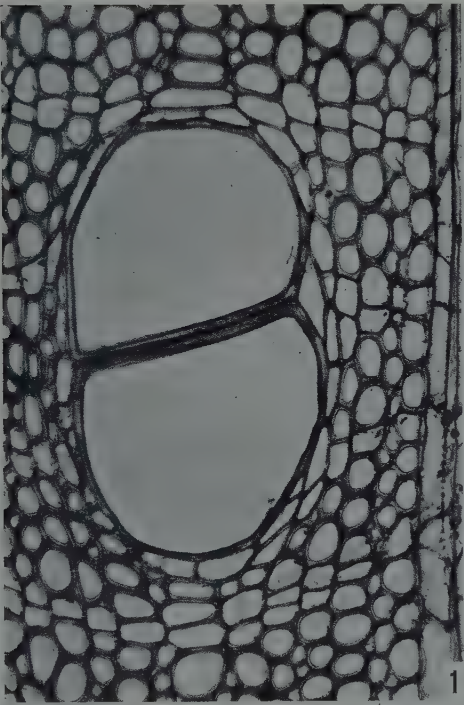
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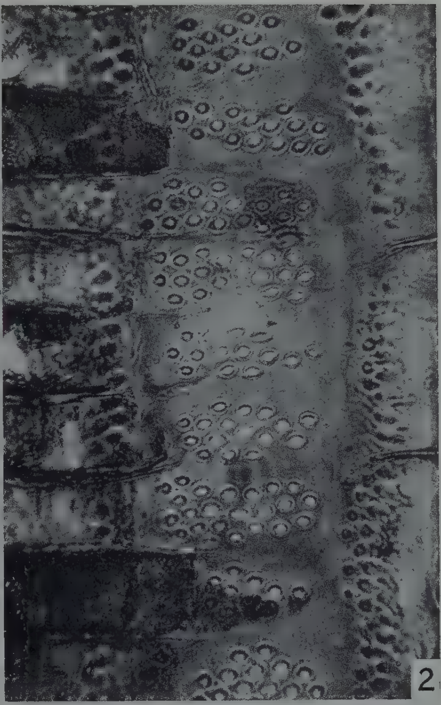
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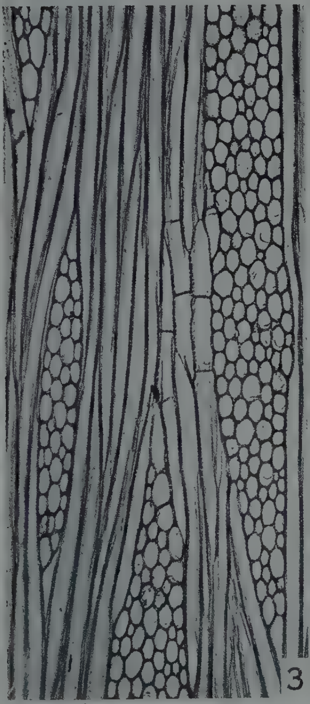
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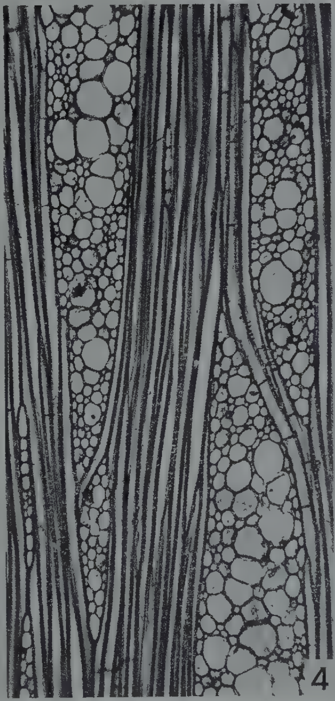
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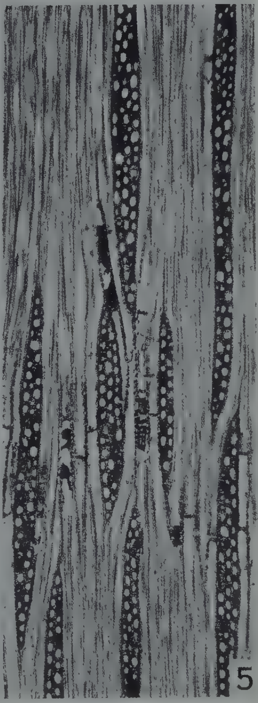
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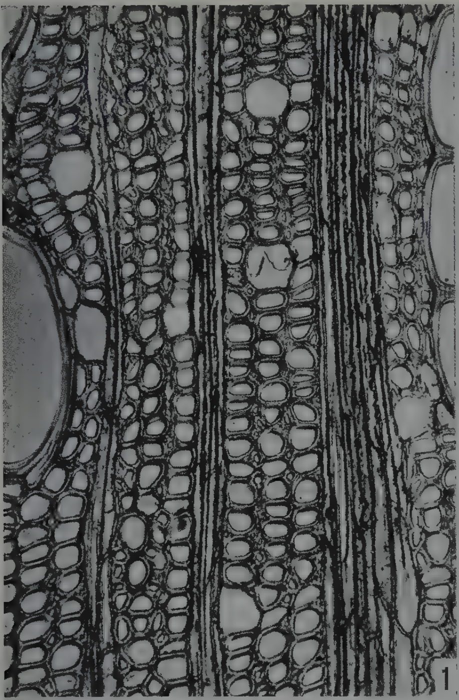
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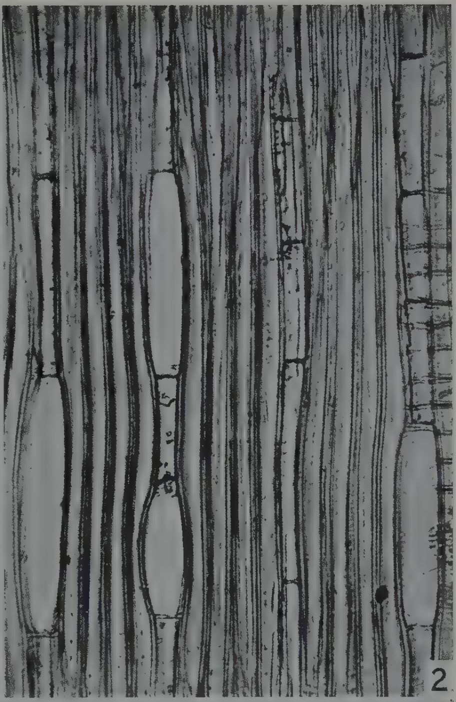
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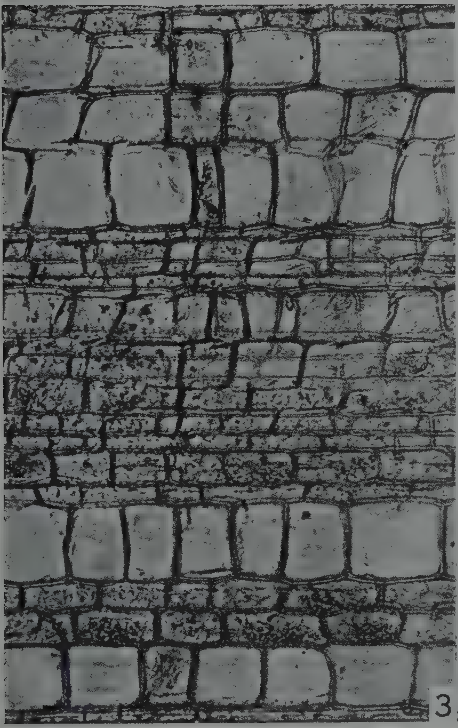
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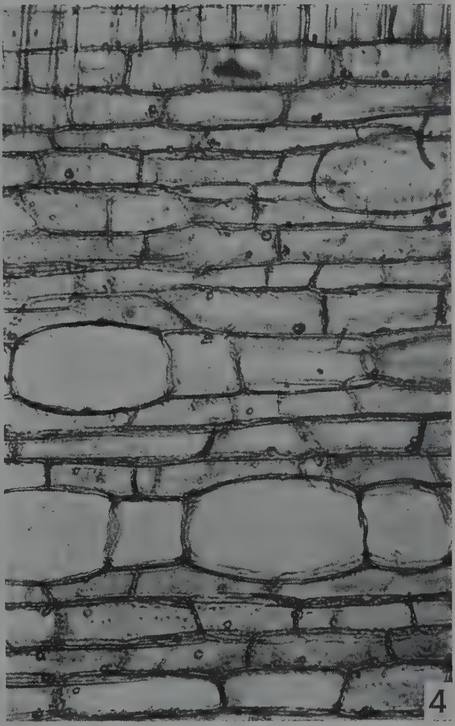
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III. Discussion of Results

The woods of the 12 genera of the Annonaceae examined show great similarity in features and can be readily recognized from timbers of all other families. Distinguishing features are:

(*a*) The presence of apotracheal parenchyma in fine, regularly spaced, concentric lines, closely spaced and interrupted by the rays. This feature alone serves to differentiate the Annonaceae from all other families.

(*b*) Vessel-ray pitting similar to the inter-vessel pitting, which is fine to minute (2-6 μ) in all genera except *Cananga, Mezzettia,* and *Xylopia.*

(*c*) Uniseriate to partly biseriate rays few in number and low, multiseriate rays generally 4-8 cells wide, weakly heterogeneous, and high, maximum number of cells varying from 60 to 130; horizontal series of square or erect cells of greater vertical dimension than normal procumbent cells present in two genera.

(*d*) The presence of oil cells in both vertical and ray parenchyma in three genera.

(*e*) Vessels seldom touching rays; pits to ray cells rare; because of this and small aperture size of vessel-ray pits, tyloses are absent (Chattaway 1949).

Oil cells are present in some genera of the Annonaceae; in this investigation solitary oil cells of the distended type were observed both in the rays and in the vertical parenchyma in *Cyathocalyx,* in vertical parenchyma in *Polyalthia* (one species) and *Cananga,* and in ray parenchyma in *Mezzettia.* Hess (1946) reports their presence in three genera, including *Xylopia,* in the vertical parenchyma and four genera, including *Xylopia,* in the ray parenchyma. Cells containing a yellowish substance resembling oil were observed among the normal ray and vertical parenchyma cells in *Alphonsea.*

The range of wood characters and properties revealed by the species of some of the larger genera is as great as that between many genera in the family. The only separable genera are *Cananga, Cyathocalyx,* and *Mezzettia,* which, to varying degrees, show paratracheal to vasicentric parenchyma as well as the apotracheal type common to all genera of the family. Small crystals were abundant in the rays of *Goniothalamus* and in rays and vertical parenchyma of *Papualthia*; Metcalfe and Chalk (1950) mention the presence of crystals also in *Alphonseopsis* and *Hornschuchia,* but state that they are typically absent in the family as a whole. Hess (1946) records the presence of scattered crystals occasionally present in the rays and rare in the parenchyma of one genus, *Rollinia.*

Acknowledgments

Material used in the survey of these two families was taken from the standard collection of the Division of Forest Products, which includes various authenticated specimens received on an exchange basis from forestry authorities in Indonesia and the Philippines. Special reference, however, must be made to specimens of Malayan timbers received through the courtesy of Mr. H. E. Desch;

to specimens of New Guinea timbers kindly made available by Mr. C. E. Lane-Poole collected during his survey in that region in 1924; to specimens from the Waterhouse collection (see Record 1945) in New Guinea and the Solomon Is. supplied by the late Dean S. J. Record of the Yale School of Forestry; to specimens received from North Borneo through the courtesy of Mr. H. G. Keith, Conservator of Forests, North Borneo; to specimens of timber from New Guinea and neighbouring islands collected by Australian Army Forestry units during the Pacific war; to material from this area received from Mr. J. B. McAdam, Director of the Forests Department of the Papua-New Guinea Administration; to specimens from the British Solomon Is. collected by Mr. F. S. Walker in 1945 and 1946.

The botanical determinations of the material from New Guinea collected by Mr. C. E. Lane-Poole and by the Australian Army and of that from the British Solomon Is. collected by Mr. F. S. Walker were carried out by the late Mr. C. T. White, Government Botanist, Brisbane; recent material from the New Guinea area has been identified by Mr. J. S. Womersley, Forest Botanist with the Department of Forests, New Guinea.

The authors wish to express their thanks to Miss Margaret Cooper and Miss Margaret Marfleet for carrying out much of the preliminary examinations of the various wood specimens.

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Explanation of Plates 1-9

Plate 1

Fig. 1.—*Hunteria zeylanica* (Retz.) Gaud. ex Thw. Transverse section showing extremely small solitary pores and diffuse to reticulate parenchyma. × 25.

Fig. 2.—*Alstonia villosa* Bl. Transverse section showing pore size and arrangement, thick-walled fibres, and diffuse to reticulate parenchyma. × 25.

Fig. 3.—*Ervatamia punctulata* (Warb.) Mgf. Transverse section showing small pores in long radial multiples and comparatively wide rays tending to two widths. × 25.

Fig. 4.—*Wrightia millgar* F.M.Bail. Transverse section showing pore arrangement and size and diffuse to reticulate parenchyma. × 25.

Plate 2

Fig. 1.—*Cerbera floribunda* K.Schum. Transverse section showing characteristic pore arrangement and fine rays. × 25.

Fig. 2.—*Cerbera manghas* L. Transverse section showing pore size and grouping and bands of parenchyma. × 25.

Fig. 3.—*Dyera costulata* Hook.f. Transverse section showing comparatively large pores and fine uniseriate bands of reticulate parenchyma. × 25.

Fig. 4.—*Alstonia scholaris* R.Br. Transverse section showing large pores and bands of parenchyma. × 25.

Plate 3

Fig. 1.—*Alstonia scholaris* R.Br. Radial section showing vessel-ray pitting typical of the family. × 320.

Fig. 2.—*Dyera costulata* Hook.f. Tangential section of large latex tube in ray. × 200.

Fig. 3.—*Alstonia scholaris* R.Br. Tangential section of ray with small latex tube. × 220.

Fig. 4.—*Cerbera floribunda* K.Schum. Radial section showing simple perforation plate with wide and prominent rim characteristic of the family. × 410.

Plate 4

Fig. 1.—*Rejoua aurantiaca* Gaud. Tangential section showing septate fibres containing elongated crystals. × 200.

Fig. 2.—*Rejoua aurantiaca* Gaud. Radial section showing enlarged marginal upright cells in the rays, containing oil or mucilage. × 200.

Fig. 3.—*Ervatamia punctulata* (Warb.) Mgf. Radial section showing characteristic crystal-bearing marginal ray cells. × 200.

Fig. 4.—*Wrightea millgar* F.M.Bail. Radial section showing chambered, procumbent, crystal-bearing cells in ray.

Plate 5

Fig. 1.—*Cerbera floribunda* K.Schum. Tangential section showing uniseriate to partly biseriate rays. × 100.

Fig. 2.—*Ervatamia punctulata* (Warb.) Mgf. Tangential section showing multiseriate, heterogeneous rays with long, uniseriate margins. × 100.

Fig. 3.—*Dyera lowii* Hook.f. Longitudinal section showing numerous small but distinctly bordered pits in fibres. × 450.

Fig. 4.—*Wrightia millgar* F.M.Bail. Radial section of disjunctive upright ray cells. × 250.

Plate 6

Fig. 1.—*Alstonia spathulata* Bl. Transverse section of stem wood showing pore and parenchyma distribution. × 25.

Fig. 2.—*Alstonia spathulata* Bl. Transverse section of root wood showing reduction of pores and thin-walled, much enlarged fibres. × 25.

Fig. 3.—*Alstonia scholaris* R.Br. Longitudinal tangential face of wood showing latex traces typical of several genera.

Fig. 4.—*Alstonia spathulata* Bl. Macerated fibres from root wood showing characteristic shape and abundance of pitting. × 80.

PLATE 7

Fig. 1.—*Xylopia dehiscens* (Blanco) Merr. Transverse section showing pore size and arrangement, and regular fine bands of parenchyma. × 25.

Fig. 2.—*Cyathocalyx polycarpum* White and Francis. Transverse section showing pore arrangement and reticulate parenchyma; note oil cells in rays. × 25.

Fig. 3.—*Cananga odorata* (Lamk.) Hook.f. et Thoms. Tangential section showing comparatively coarse inter-vessel pitting. × 500.

Fig. 4.—*Phaeanthus macropodus* (Miq.) Diels. Tangential section showing minute inter-vessel pitting. × 500.

Fig. 5.—*Goniothalamus grandiflorus* (Warb.) Boerl., showing small crystals in the ray cells typical of this genus and *Papualthia*. × 375.

PLATE 8

Fig. 1.—*Cyathocalyx* sp. nov. Transverse section showing apotracheal bands of parenchyma and vasicentric parenchyma. × 180.

Fig. 2.—*Xylopia fusca* Maing. ex Hook.f. Radial section showing vessel-ray pitting typical of the family. × 400.

Figs. 3-5.—Comparison of ray type in the family:

Fig. 3.—*Cananga odorata* (Lamk.) Hook.f. et Thoms, showing weakly heterogeneous rays and thin-walled ray cells. × 180.

Fig. 4.—*Polyalthia holtzeana* F.Muell., showing typical enlarged series of cells giving heterogeneous aspect to rays of *Polyalthia*. × 180.

Fig. 5.—*Xylopia* sp., showing characteristic small thick-walled ray cells and homogeneous rays. × 180.

PLATE 9

Fig. 1.—*Cyathocalyx polycarpum* White and Francis. Transverse section showing oil cells in vertical parenchyma. × 180.

Fig. 2.—*Polyalthia oblongifolia* Burck. Radial section showing oil cells in vertical parenchyma. × 180.

Fig. 3.—*Polyalthia holtzeana* F.Muell. Radial section of ray showing horizontal series of enlarged cells (cf. Plate 9, Fig. 4). × 180.

Fig. 4.—*Cyathocalyx polycarpum* White and Francis. Radial section of ray showing oil cells. × 180.

THE OCCURRENCE OF HEARTWOOD CRYSTALS IN CERTAIN TIMBERS

By M. MARGARET CHATTAWAY[*]

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Summary

Crystals of a very characteristic shape and colour have been observed in the heartwood of 52 species from 19 different families. They are quite distinct in composition and appearance from the crystals of calcium oxalate that occur in the wood of many timbers, and they have never been seen in sapwood.

The crystals appear first in the ray cells, where these are in contact with a vessel element. The area in which the crystals occur extends through all the tissues of the heartwood. The shape they take is partially dependent on the tissue in which they occur. They have frequently been found in close association with fungal hyphae.

Their distribution has been studied intensively in *Eucalyptus hemiphloia* F. Muell. and *E. sideroxylon* A. Cunn., in which species they occur from the pith to a short distance from the outer edge of the heartwood and from the base of the tree to the upper limit of the heartwood. In a random selection of discs from other species of the genus *Eucalyptus* the crystals have a similar distribution within the heartwood.

The crystals in *E. hemiphloia* have given identical chromatograms with crystals of ellagic acid, and it is probable that crystals in other Myrtaceae are of a similar nature.

Further research is needed for identification of the fungi with which these crystals are associated, and to determine the chemical composition of the crystals and of the heartwood extractives of the woods in which they occur.

I. INTRODUCTION

During an investigation of some Australian timbers, it was noted that the heartwood regularly contained masses of yellowish brown crystals of very characteristic form and distribution. These crystals do not resemble the calcium oxalate crystals that are so common a feature of many woods, either in their appearance, properties, or in their development. They have never been observed in sapwood.

Although they occur freely in woods from all parts of the world, no reference whatsoever to their occurrence has been found in the literature. That they have often been observed by wood anatomists cannot be doubted, as they are both widespread and conspicuous in wood sections. Their neglect by wood anatomists is surprising, but may be due to their frequent occurrence near areas of fungal attack, which are usually avoided when blocks are prepared for routine sectioning. It is their invariable appearance so close to the outer edge of the heartwood of certain genera, as well as their complete neglect by earlier workers, that has prompted the present investigation.

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[*] Division of Forest Products, C.S.I.R.O., South Melbourne.

II. Nature and Appearance of the Crystals

Throughout this investigation the term "heartwood crystals" is used to denote the yellowish brown crystalline masses which have, so far, been observed only in heartwood.

The chemical composition of all these crystals is not yet fully understood, nor is it known yet whether they are the same in all the families in which they have been found. Their appearance under the microscope is, however, so characteristic that they are at once recognizable in all the different tissues in which they occur. Crystals extracted from *Eucalyptus hemiphloia* and crystals known to be ellagic acid have been examined simultaneously by partition chromatography (Hillis 1951) and have given identical chromatograms. It is therefore probable that the crystals in *E. hemiphloia* are ellagic acid. Chromatographic examination indicates that crystals in other of the Myrtaceae are also ellagic acid. Very few of the other genera in which the crystals occur have been examined chromatographically, but the fluorescence and R_F value observed in these few indicate that ellagic acid is present in the heartwood. Furthermore, ellagic acid has been shown to be absent from a number of other species which are among those in which crystals have not been observed.

Heartwood crystals are insoluble in hydrochloric acid but readily soluble in a dilute solution of sodium hydroxide. They are birefringent under polarized light and may take many different shapes, which are apparently related to the tissue in which they occur. They can be seen in both stained and unstained sections of the wood. They may occur as solitary crystals (Plate 1, Figs. 1 and 3), but are more commonly in aggregates, appearing as fan-shaped masses in ray and parenchyma cells (Plate 1, Figs. 2 and 4) and as plates (Plate 2, Figs. 1 and 2) or bundles of needle-shaped crystals in the fibres. In the tyloses in vessel lumina they often occur as spherical masses (Plate 2, Fig. 4).

Heartwood crystals may occur in any tissues of the heartwood, and often have the appearance of spreading from a focal point in the cell, filling some cells completely, and spreading, via the pits, to adjacent cells (Plate 2, Figs. 3 and 4).

The crystals differ from the calcium oxalate crystals that are commonly found in ray and parenchyma cells, and sometimes in fibres, not only in their distribution, colour, and chemical composition but in the manner of their formation. Calcium oxalate crystals appear to be by-products of the active metabolism of the cambial layer, for they are laid down very early in the life of the parenchyma and ray cells. Sections through the cambial layer of a crystalliferous wood show that the calcium oxalate crystals appear in their containing cells immediately these are cut off from the cambium, and that the cells in which they are deposited often continue as living cells for a considerable time—often, in fact, throughout the sapwood. This is shown both by the very thick walls that are formed around calcium oxalate crystals or on the walls of the containing cell, and also by the presence of nuclei in the part of the cell that is not occupied by the crystal (Plate 3, Fig. 1). The yellow-brown heartwood crystals have never been observed in living cells; they do not appear in the cell until it is moribund or dead, i.e. at the time of heartwood formation. When radial sections passing through the sapwood-heartwood line are examined, the crystals first appear in the ray cells of the heartwood, usually where the ray is contiguous with a vessel (Plate 3, Figs. 2 and 3). As they develop they appear in adjacent cells (Plate 2, Figs. 4 and 5), ultimately forming quite extensive patches within the wood (Plate 3, Fig. 4); the patches of crystal become larger and more frequent towards the pith, but never fill the wood completely. Even when the wood is heavily impregnated with the crystals, they still occur as patches, with adjacent areas of the wood comparatively, sometimes even completely, free from them. Thus it appears probable that they are not a product of cell activity, but must be deposited in the cell itself and spread through the heartwood tissues by the activity of some outside organism, or by some change in the contents of the dead and drying cell. In many cases the agent is certainly a fungal hypha.

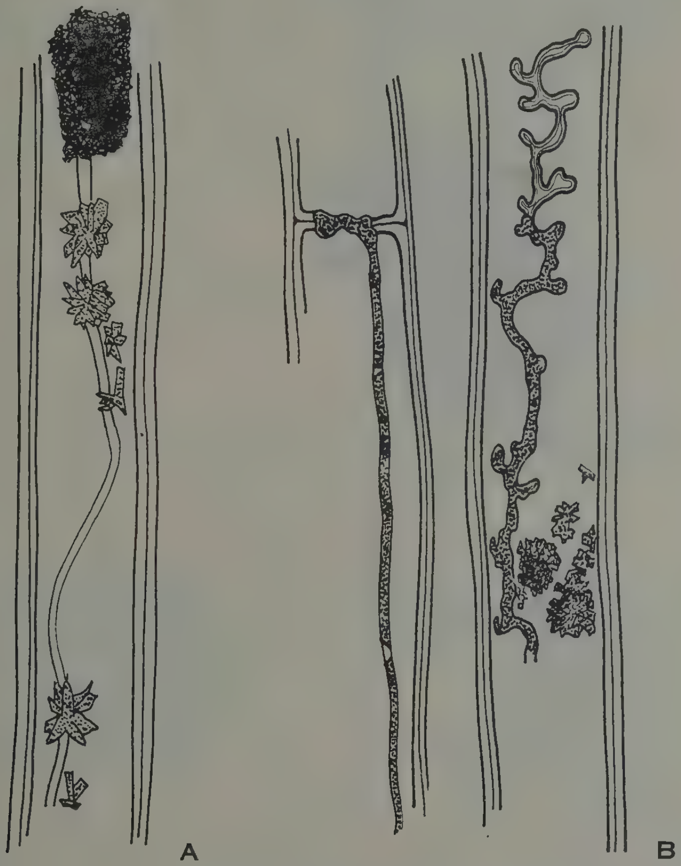

Fig. 1.—*A, Sloanea woollsii* F. Muell., fungal hypha with attached crystal clusters. × 1100 approx.

B, Canarium acutifolium (DC.) Merrill, fungal hyphae with crystalline substance deposited within them. × 1500 approx.

III. Association with Fungi

The association of fungal hyphae with heartwood crystals was first observed in *Sloanea woollsii* F.Muell. As is shown in Figure 1*A* a crystal mass is associated with a longitudinally running hypha, along part of which attached clusters of crystals can be seen. Plate 4, Figure 1, of *Sloanea* sp., and Figure 2 show two typical fan-shaped crystal masses in adjacent ray cells. The fungal hypha can be seen passing through the upper crystal mass towards a pit in the wall which separates this from the lower crystal mass in the adjacent cell. Plate 4, Figure 3, shows some fibres from *Eucalyptus marginata* Sm., through which a fungal hypha has penetrated laterally. The lumina of the fibres are filled with a solid mass of kino, within which crystal masses have developed along the track of the hypha. Another hypha, also from *E. marginata,* is shown in Plate 4, Figure 2. In this the crystal mass is forming along the length of a hypha as in the figure of *Sloanea woollsii,* but the incrusting crystals are more massed and tend to obscure the hypha. Plate 4, Figure 4, shows a group of crystals from some liquid kino that exuded from a gum pocket in the heartwood of *Eucalyptus obliqua* L'Herit.; many similar crystals were observed, often with a fungal hypha still attached. A similar association of small groups of almost isolated crystals in the ray cells of *Homalanthus* sp. is shown in Plate 5, Figure 1. The other figures on this plate show more examples of hypha and crystal association, an association that has been observed so often that it is difficult to avoid drawing the conclusion that it is not fortuitous, but that the hypha is responsible for the formation of the crystal masses. An even closer association was observed in *Canarium acutifolium* (DC.) Merrill (Figs. 1*B* and 3*A*) and *Elaeocarpus eumundi* F. M. Bailey (Fig. 3*B*). In these two woods the crystals are small and tend to form very dense masses within the containing cells. But in addition to this, crystals also form within the hyphae themselves, causing them to become markedly birefringent under polarized light. The portions of the hypha that are filled with crystals can be clearly distinguished under both ordinary and polarized light from those that do not contain them. In some woods the heartwood crystals form not only inside the cells, but along the intercellular membrane,

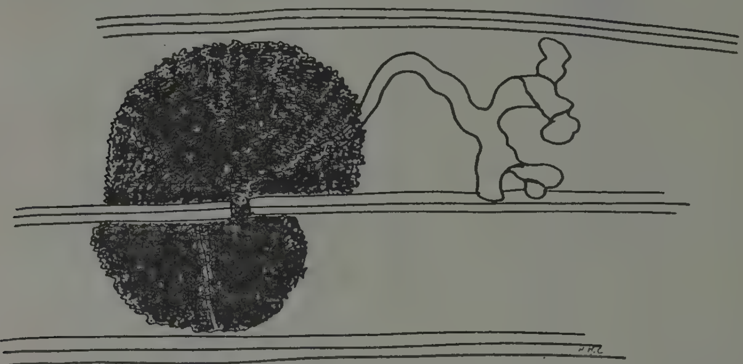

Fig. 2.—*Sloanea* sp., fan-shaped crystal clusters associated with a fungal hypha. × 1025 approx.

filling the intercellular spaces and, in extreme cases, forcing the cells apart and enlarging the intercellular spaces between ray and parenchyma cells (Figs. 4*A*, 4*B*).

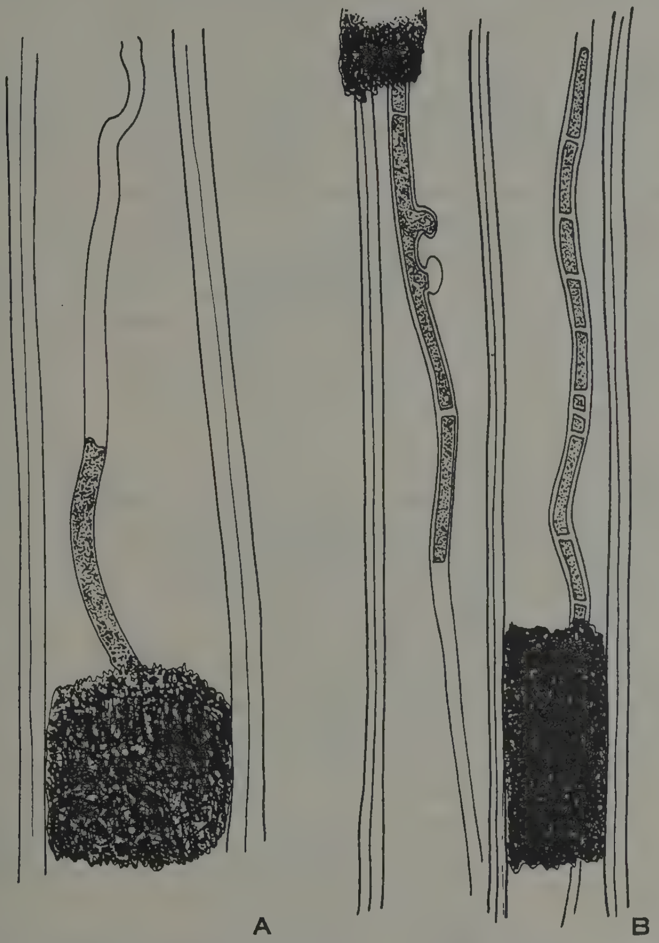

Fig. 3.—Crystal clusters attached to, and crystalline substance deposited within fungal hyphae:

A, *Canarium acutifolium* (DC.) Merrill. × 1100 approx.
B, *Elaeocarpus eumundi* F. M. Bailey. × 750 approx.

The association of the heartwood crystals with fungal hyphae is, however, not always as easy to observe as in the examples illustrated above. In many species the hyphae are extremely fine and very difficult to stain, so that they are barely visible in the cells. Although in some species of *Eucalyptus* the attachment of the crystals to fungal hyphae appears clearly, there are many species in which the hyphae are extremely difficult to see, so difficult in fact that their presence can only be inferred from "tracks" that can be seen through the dry heartwood kino and on the cell walls. In these woods, too, the fungi are very difficult to culture and at present the association of crystals and fungi in such woods rests only on surmise and on the complete similarity of the crystal distribution and structure to those in which the hyphae are more easily seen.

IV. Distribution among Families

The crystals have been found in 19 families, in the genera shown in Table 1. The list is not exhaustive as there are genera of which no material, or only sapwood, was available.

The crystals have never been observed in the families listed in Table 2.

Table 1

FAMILIES AND GENERA IN WHICH THE CRYSTALS HAVE BEEN OBSERVED

Family	Genera
Aceraceae	*Acer*
Alangiaceae	*Alangium*
Anacardiaceae	*Dracontomelum*, *Euroschinus*, *Gluta*, *Melanorrhoea*, *Microstemon*, *Pentaspodon*, *Pistacia*, *Rhus*, *Rhodosphaera*
Burseraceae	*Boswellia*, *Canarium*, *Garuga*, *Haplolobus*
Combretaceae	*Anogeissus*, *Lumnitzera*, *Terminalia*
Cornaceae	*Cornus*
Cunoniaceae	*Ceratopetalum*
Datiscaceae	*Octomeles* (not typical and not in all slides)
Dipterocarpaceae	*Dryobalanops*, *Shorea*
Elaeocarpaceae	*Elaeocarpus*, *Sloanea*
Euphorbiaceae	*Antidesma*, *Bridelia*, *Homolanthus*, *Petalostigma*
Fagaceae	*Castanea*, *Castanopsis*, *Nothofagus*, *Pasania*, *Quercus*
Juglandaceae	*Juglans*
Myristicaceae	*Coelocaryon*
Myrtaceae	*Angophora*, *Acmena*, *Backhousia*, *Callistemon*, *Cleistocalyx*, *Eugenia*, *Eucalyptus*, *Melaleuca*, *Syncarpia*, *Syzygium*, *Tristania*
Olacaceae	*Ochanostachys*
Oliniaceae	*Olinia*
Sonneratiaceae	*Duabanga*, *Sonneratia*
Verbenaceae	*Vitex* (?)

V. Distribution of the Crystals in the Tree

As has been mentioned before, no comparable crystals of this kind have ever been observed in the sapwood. Their distribution within the heartwood has been studied in several species of *Eucalyptus*, both from the sapwood-heartwood line to the pith and from the base of the tree to the upper limit of the heartwood development. The results of these studies are shown in Figures 4, 5, and 6. In every species examined the crystals first appeared within a short distance of the sapwood-heartwood line, sometimes within a few millimetres of it. They are formed at approximately the same distance from the sapwood-heartwood line from the base of the tree to the upper limit of heartwood development, appearing first as small, sparsely scattered crystals in the ray cells (Plate 3, Figs. 2 and 3), usually where a ray is contiguous with a vessel, becoming more frequent inwards towards the pith and filling other tissues indiscriminately (Plate 3, Fig. 4). This pattern has been more or less uniform in all the woods examined, and Figure 6 shows a series of diagrams similar in detail to those in Figures 4 and 5, but representing sections taken on different radii of a single disc from the stem of each of various *Eucalyptus* species.

TABLE 2

FAMILIES IN WHICH THE CRYSTALS HAVE NOT BEEN OBSERVED

Acanthaceae
Akaniaceae
Aquifoliaceae
Annonaceae
Apocynaceae
Araliaceae
Betulaceae
Balanopsidaceae
Berberidaceae
Bombacaceae
Boraginaceae
Capparidaceae
Caprifoliaceae
Casuarinaceae
Celastraceae
Cercidiphyllaceae
Chenopodiaceae
Chloranthaceae
Cochlospermaceae
Compositae
Corynocarpaceae
Crypteroniaceae
Dilleniaceae
Ebenaceae
Epacridaceae
Erythroxylaceae
Eucryphiaceae
Flacourtiaceae
Guttiferae
Himantandraceae
Icacinaceae
Lauraceae
Lecythidaceae
Leguminosae
Loganiaceae
Lythraceae
Magnoliaceae
Malvaceae
Melastomaceae
Meliaceae
Moraceae
Monimiaceae
Myoporaceae
Myrsinaceae
Nyssaceae
Ochnaceae
Oleaceae
Phytolaccaceae
Piperaceae
Pittosporaceae
Platanaceae
Polygalaceae
Proteaceae
Rhamnaceae
Rhizophoraceae
Rosaceae
Rubiaceae
Rutaceae
Santalaceae
Sapindaceae
Sapotaceae
Saxifragaceae
Scrophulariaceae
Solanaceae
Staphylleaceae
Styracaceae
Sterculiaceae
Tamaricaceae
Theaceae
Thymeliaceae
Tiliaceae
Ulmaceae
Urticaceae
Violaceae
Vochysiaceae
Zygophyllaceae

VI. DISCUSSION

As the result of this survey of heartwood crystals two striking facts have emerged:

(*a*) The constancy of the occurrence of the crystalline masses of a very characteristic shape in the heartwood of certain species;

(*b*) The frequent occurrence of the crystals within a few millimetres of the outer limit of the heartwood.

Heartwood crystals are not merely extraneous bodies that are found occasionally in the wood of certain trees; they have been found consistently in the heartwood of 165 different species of *Eucalyptus* and their distribution in the trunks of four different trees (two of *E. hemiphloia* and two of *E. sideroxylon*) was an even one throughout the heartwood from the pith to within a few millimetres of its outer edge, and from the base of the tree to the upper limit of heartwood formation; in other species of *Eucalyptus* a random selection of discs has always given a similar pattern of distribution of the heartwood crystals.

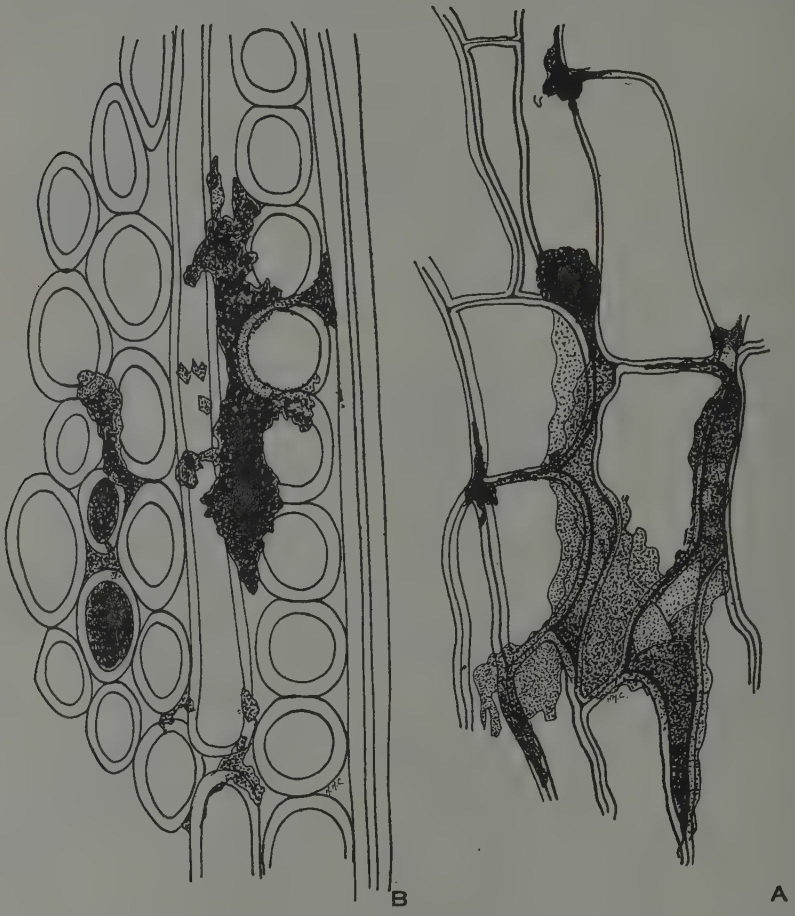

Fig. 4.—*Quercus stellata* Wangh. Crystal masses in intercellular spaces between ray cells (*A*), and parenchyma cells (*B*). × 1000 approx.

The cells in which the heartwood crystals form are dead cells, and the crystals cannot be considered as by-products of cell metabolism, yet they appear to spread from cell to cell and tissue to tissue in a regular manner. In every sample in which serial sections have been made from the outside of the stem to the pith the same pattern of development has been observed. Anatomical investigation alone cannot provide an explanation of their presence, but certain hypotheses in connection with their formation may be discussed:

(i) That they are the result of a purely chemical change in the cells of the heartwood, consequent upon their death and the decomposition of their contents. Such a hypothesis must disregard the numerous instances in which the crystals are so closely associated with the fungal hyphae or must regard the

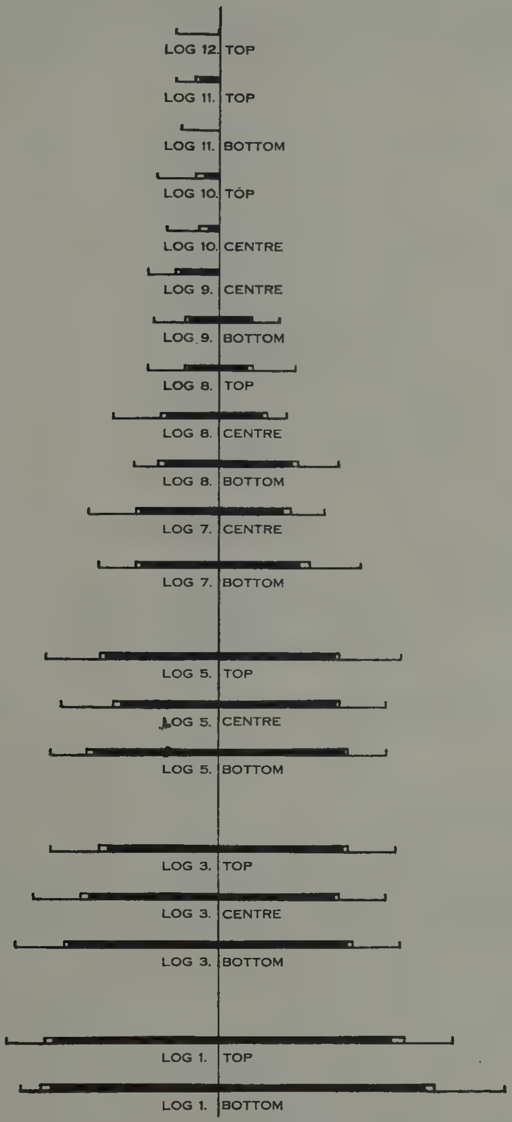

Fig. 5.—*Eucalyptus hemiphloia* F. Muell. Distribution of crystals in the heartwood from the base of the tree to the upper limit of heartwood formation. (Solid black = tissue containing crystals. Double line = heartwood. Single line = sapwood. Each line represents to scale a stem radius.)

part the hyphae play as a purely passive one, considering them merely as the focal point for crystal formation from a supersaturated solution of ellagic acid, the crystals forming around hyphae already present in the tissues. In such a case it is difficult to understand why the pattern of development of the crystals should always take the same form, whether fungal hyphae can be seen in the cells or not.

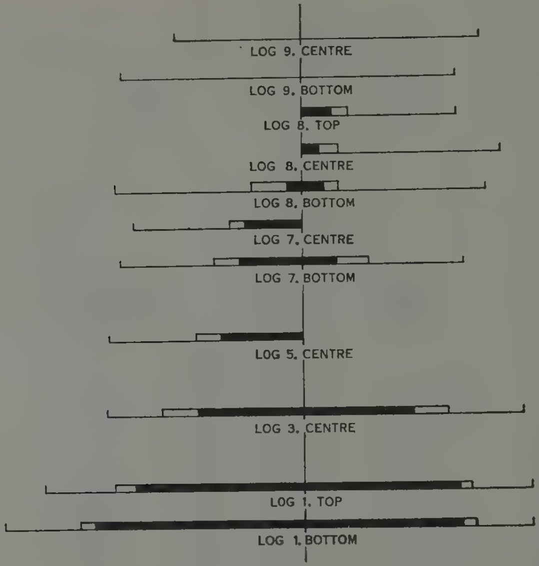

Fig. 6.—*Eucalyptus sideroxylon* A. Cunn. As for Figure 5.

(ii) That they are the result of fungal activity, the fungus advancing through the dead tissues of the heartwood, using the tannins of the heartwood, producing heartwood crystals as a by-product of its metabolism.

In favour of this hypothesis is the common association of the crystals with fungal hyphae, and their observed manner of spreading from cell to cell via the pits, thin areas in the cell wall that are very commonly the path of the spread of fungal hyphae.

Against it is the fact that although in some species the association of fungus and crystal can be easily seen, in others it is most difficult, often impossible, to see it. Sometimes the hyphae cannot be seen with any certainty even when the crystals have been dissolved from the cells with caustic potash. Furthermore, cultures from fresh material of wood that contains the crystals and in which the hyphae are difficult to see sometimes remain sterile, even when patches of crystal-containing material are known to be relatively frequent in adjacent tissue. In such species the fungus has yet to be found; its presence is suspected but not certain; but the development of the crystals has proved to be so similar in all the woods examined that it is difficult to envisage dissimilar causes for their presence.

The association of fungal activity with crystal formation has been noted by Cartwright in brown oak. He makes no mention of the crystals in his paper on the subject (Cartwright 1937) but the following extract from a letter shows that, in his material, too, the association can be observed:

"I have made a thorough examination of unstained preparations of brown oak and have found several groups of crystals of the same type shown in your photographs, which appear to be associated with the fungus."

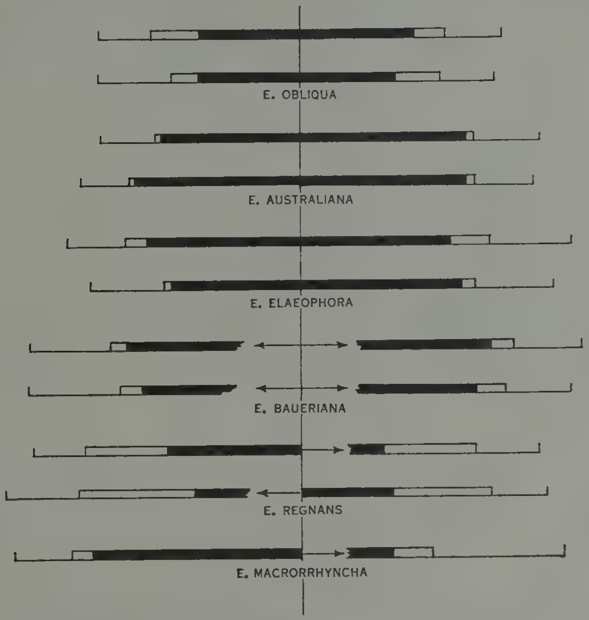

Fig. 7.—*Eucalyptus* spp. various. Distribution of crystals in discs selected at random from main trunks of the trees. Shading as for Figure 5.

The problem now offers two lines of progress, both on the mycological side:

(*a*) Further attempts to grow cultures from wood in which heartwood crystals occur, but in which the fungal association is difficult to see; and

(*b*) Cultivation of fungi from woods in which the association of fungus and crystals has already been observed, identification of the various fungi concerned, and attempts to form *in vitro* crystals similar to heartwood crystals.

VII. References

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Hillis, W. E. (1951).—*Aust. J. Appl. Sci.* 2: 385-95.

Explanation of Plates 1-5

Plate 1

Fig. 1.—*Eucalyptus muelleriana* Howitt. Solitary crystals and crystal masses in fibres. × 85.

Fig. 2.—*E. marginata* Sm. Fan-shaped crystal cluster in ray cell. × 1000.

Fig. 3.—*E. oreades* R. T. Bak. Solitary crystals in fibres. × 600.

Fig. 4.—*E. marginata* Sm. Patch of ray and parenchyma cells containing crystals. × 200.

Plate 2

Fig. 1.—*Eucalyptus polyanthemos* Schau. Plate-like and clustered crystals. × 330.

Fig. 2.—*E. muelleriana* Howitt. Plate-like crystals.

Fig. 3.—*E. globulus* Labill. Fan-shaped crystal masses, spreading from cell to cell via the pits. × 330.

Fig. 4.—*E. polyanthemos* Schau. Spherical crystal mass in tylosis. × 850.

Fig. 5.—*Syncarpia laurifolia* Ten. Fan-shaped crystals in ray cells, spreading via the pits. × 600.

Plate 3

Fig. 1.—*Acacia decurrens* Willd. Chambered parenchyma cells with calcium oxalate crystals and nuclei. × 1280.

Fig. 2.—*Eucalyptus sideroxylon* A. Cunn. Ray cell which is contiguous with a vessel, containing crystal mass.

Fig. 3.—*E. hemiphloia* F. Muell. Early stage in crystal formation, the crystal masses are confined to ray cells which are contiguous with a vessel. × 115.

Fig. 4.—*E. polyanthemos* Schau. Later stage, crystal masses in both ray and vertical tissues. × 115.

Plate 4

Fig. 1.—*Sloanea* sp. Fungal hypha in close association with two fan-shaped crystal masses. × 900.

Fig. 2.—*Eucalyptus marginata* Sm. Crystal masses traversed by fungal hypha. × 500.

Fig. 3.—*E. marginata* Sm. Fungal hypha with attached crystals. × 640.

Fig. 4.—*E. obliqua* L'Herit. Fungal hypha from liquid heartwood kino, with attached crystal cluster. × 225. [After Hillis 1951.]

Plate 5

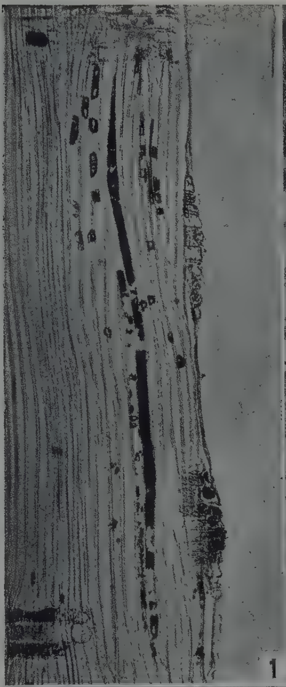
Fig. 1.—*Homalanthus* sp. Association of fungal hyphae and crystal clusters. × 540.

Fig. 2.—*Quercus lobata* Nee. As above. × 540.

Fig. 3.—*Nothofagus dombeyi* Blume. As above. × 850.

Fig. 4.—*Eucalyptus marginata* Sm. As above. × 600.

HEARTWOOD CRYSTALS IN CERTAIN TIMBERS



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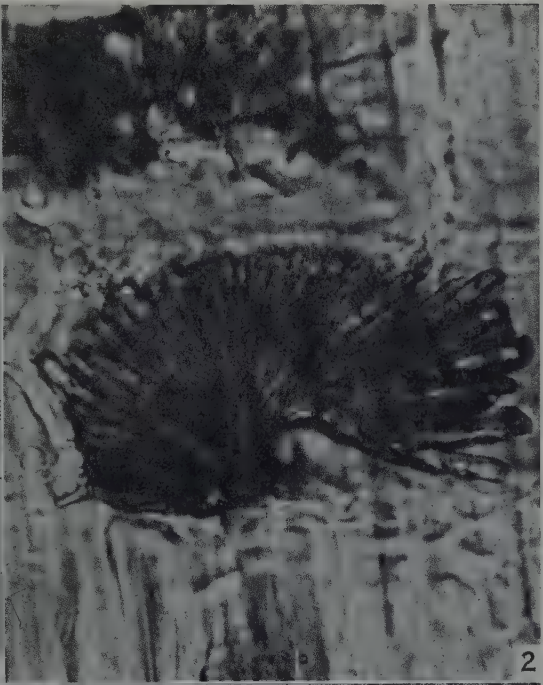

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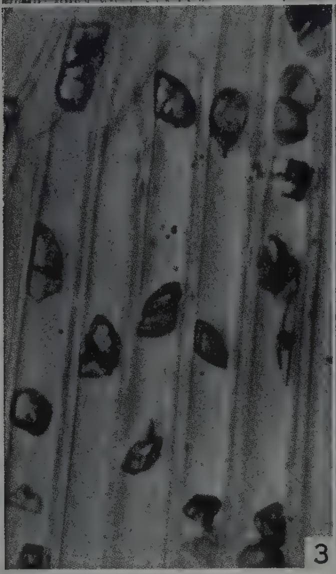

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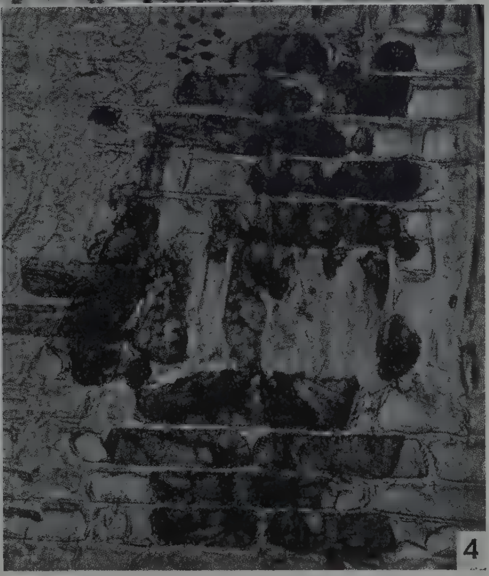

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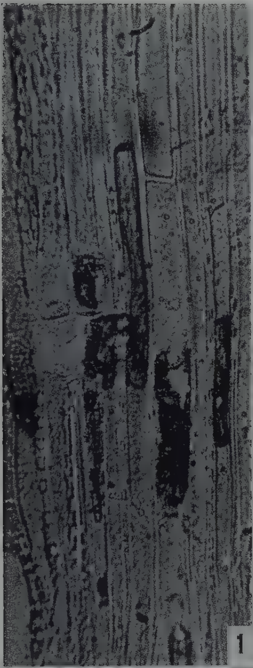
HEARTWOOD CRYSTALS IN CERTAIN TIMBERS



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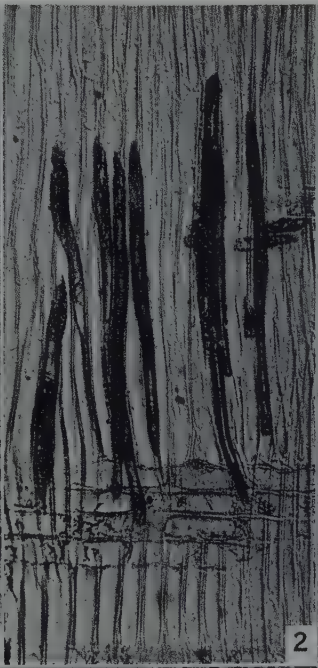

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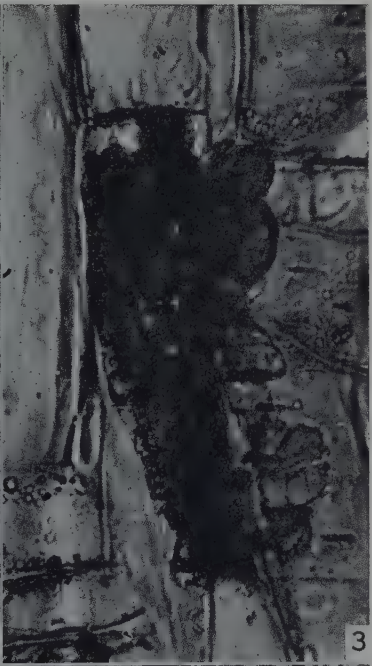

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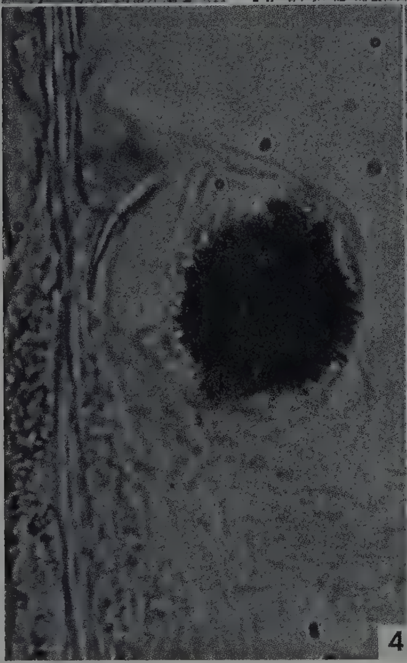

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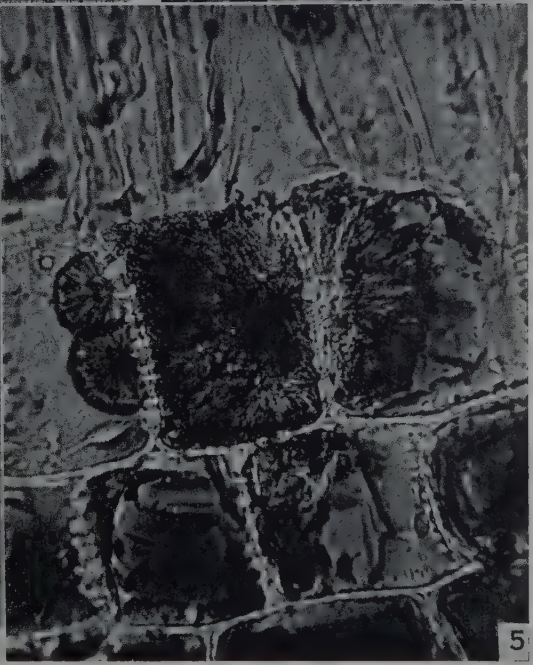

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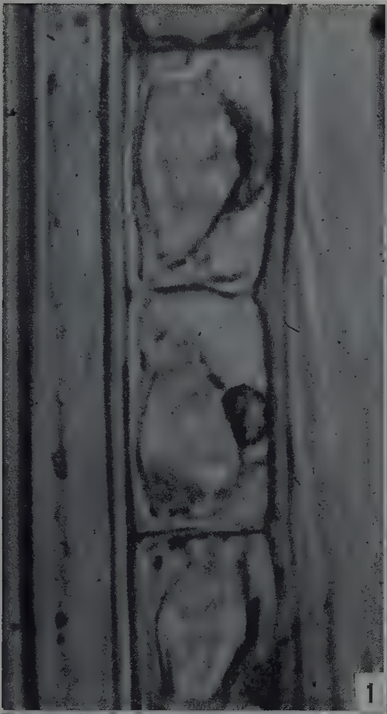
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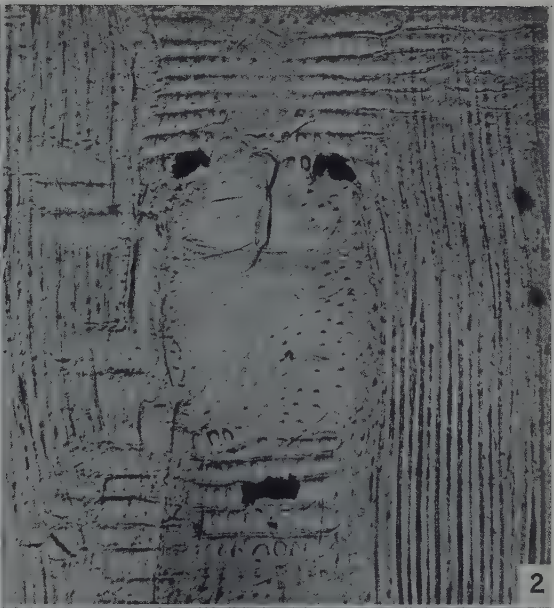
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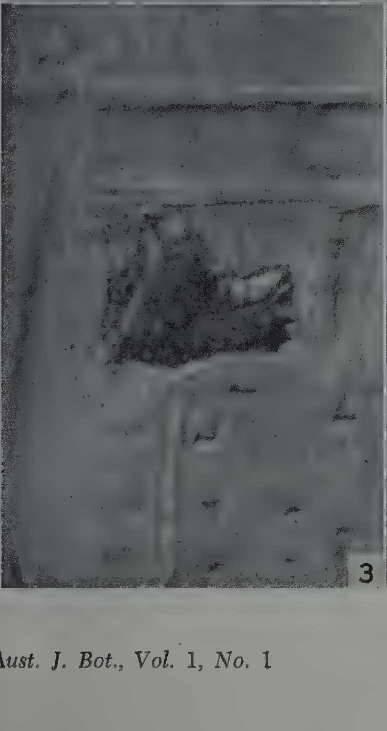
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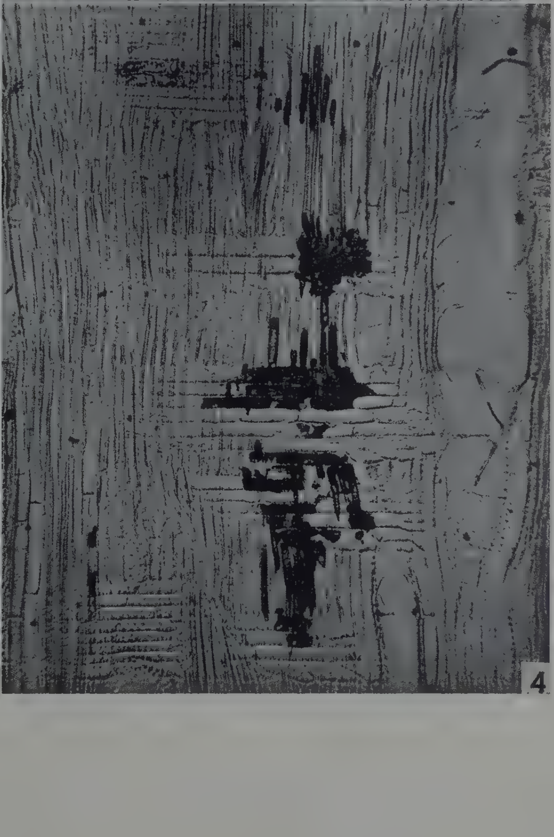
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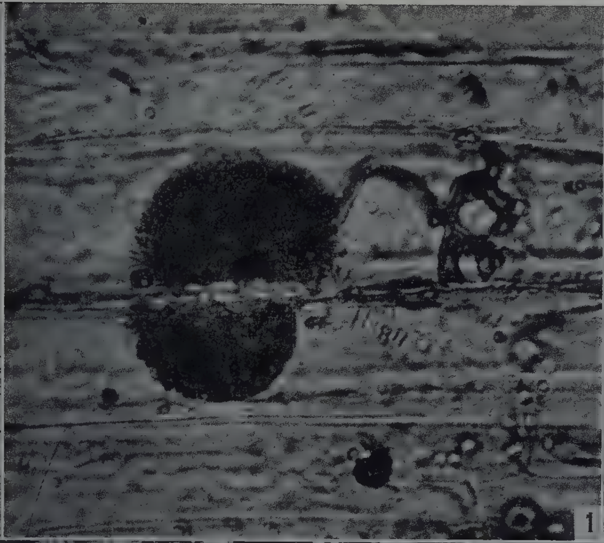

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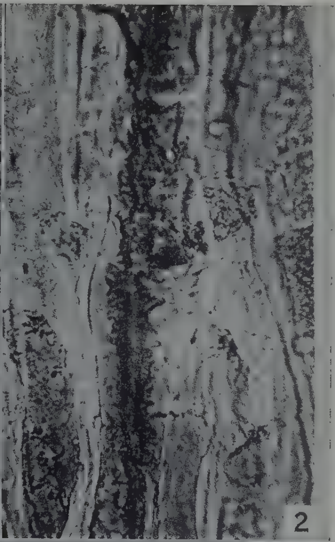

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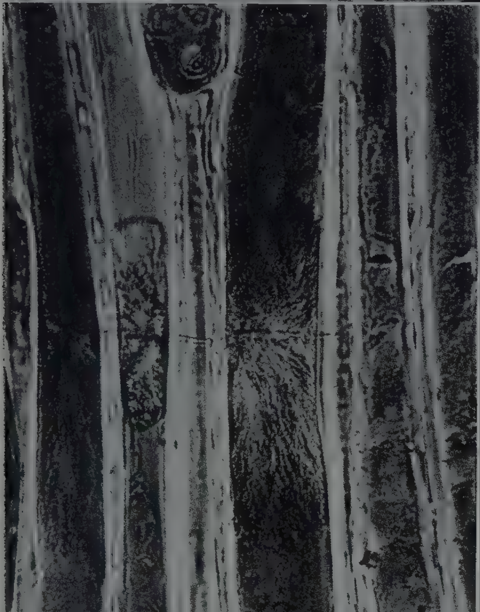

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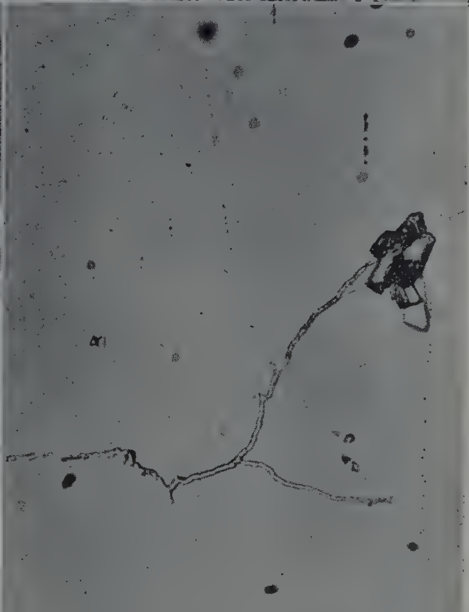

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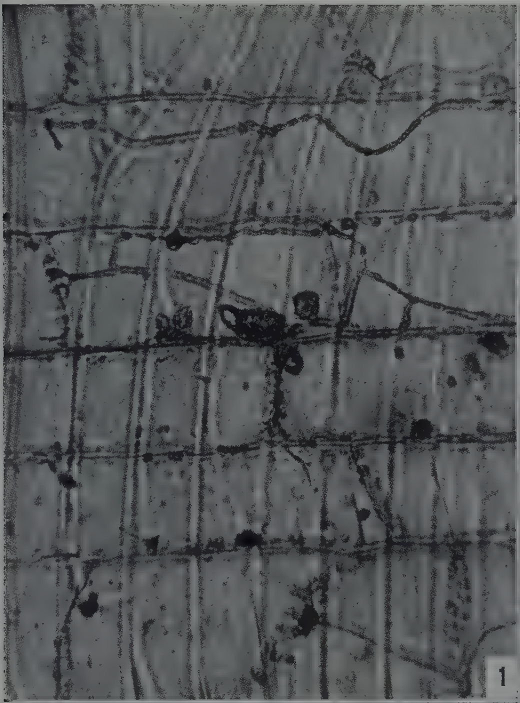
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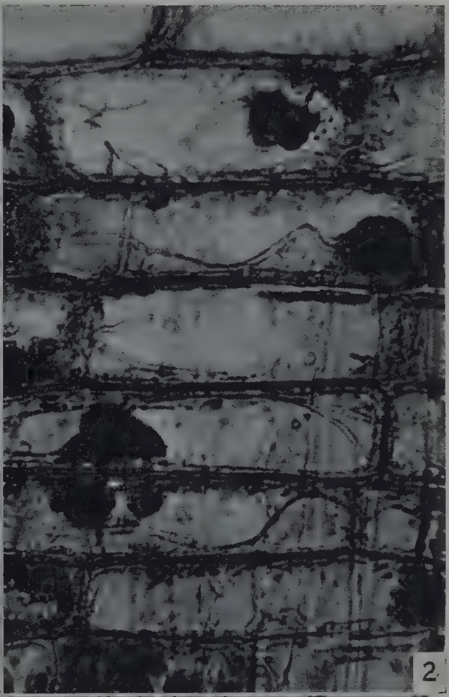
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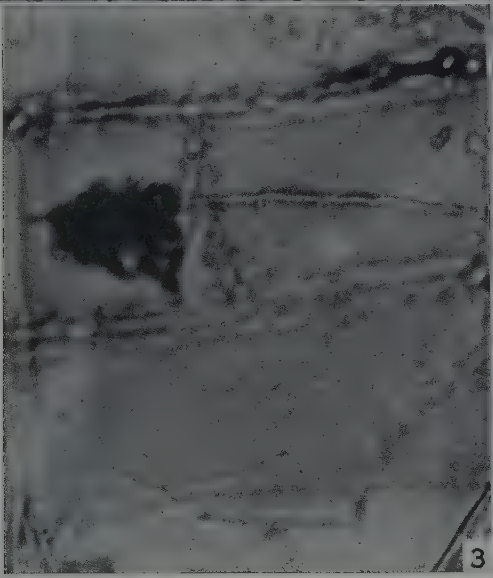
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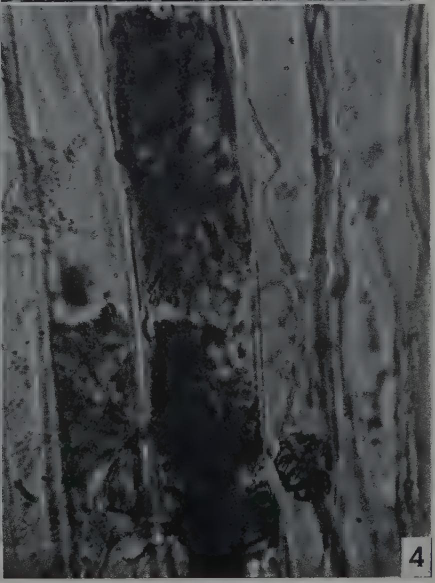
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OBJECTIVE METHODS FOR THE CLASSIFICATION OF VEGETATION

I. THE USE OF POSITIVE INTERSPECIFIC CORRELATION

By D. W. Goodall*

[*Manuscript received June* 5, 1952]

Summary

It is argued that correlations between the presence or quantity of different species recorded in quadrats imply heterogeneity in the vegetation in which the quadrats were placed. If the quadrat data can be so divided that within each subdivision no interspecific correlations occur, these subdivisions represent elementary classification units of the vegetation, and an objective classification may be arrived at if methods can be found of satisfying this requirement.

Four procedures are described for dividing a set of quadrat data into groups satisfying the above criterion of homogeneity. The simplest and apparently the most satisfactory consists in finding the most frequent species showing significant correlations with others, and separating in the first instance all quadrats containing this species. Within this group correlations are again tested, and the process is repeated until a group with no significant correlations has been extracted. All other quadrats are then lumped together and the process is begun again from the beginning. When the whole collection of quadrat data has been divided in this way into homogeneous groups, these groups are recombined where this can be done without the resulting larger group showing interspecific correlations.

The four procedures suggested are illustrated on data from a small area of the Victorian Mallee. Some of the results suggest that classification is an inappropriate method of dealing with variation in this type of vegetation, and that a coordinate treatment might be more suitable.

I. Introduction

The urge to classification lies at the roots of the development of language and of thought itself at all but the most primitive levels. Until some degree of order has been conferred by classification on the complex and manifold objects of sense, ordered thought about them is virtually impossible. And with vegetation, as with other natural objects, Man early felt the need to classify. At first only the most obvious features of its general appearance were taken into account, in distinguishing forests from moors and grassland from heath; but when science began in the nineteenth century to concern itself with vegetation (as distinct from the plant species which compose it) it was found that the distinctions recognized in common speech did not deal adequately with the variations found. Consequently, there began the spate of systems for the classification of vegetation which is still in full flow.

Many different features of vegetation have been proposed as bases for systems of classification. Some investigators have even preferred to use features

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* Botany Department, University of Melbourne. Present address: University College of the Gold Coast, Achimota, Gold Coast.

of the environment, postulating that these determined the distribution of the plants. Some have used the structure or the "physiognomy" of the vegetation. Most, however, have made use of the species present, either considered individually or in groups united by biological similarities or similar geographical distribution. Some have taken into account only the presence or absence of species; to others the quantitative relations among them are of first importance and the vegetation is classified by the "dominants" of the uppermost stratum or of all strata, defined either by quantity or by frequency. These various bases of classification have recently been discussed and compared by Braun-Blanquet (1951).

Most of those attempting to classify vegetation have been content to rely on visual impressions. After spending some time in the area under study, they have found themselves able to distinguish different categories of vegetation by processes partly subconscious, and they proceed to describe these categories, perhaps with the aid of detailed quantitative study of particular areas or quadrats selected as representative of them. But in time the self-critical ecologist relying thus on the "soziologische Blick" (Du Rietz 1921) or "Formensinn" (Braun-Blanquet 1921) may come to doubt the trustworthiness of his own work. Is he maintaining his standards? Do the categories he recognizes now correspond in status with those he recognized a year ago? Are preconceptions influencing his subconscious judgments and imparting a bias to them? So long as he relies on visual impressions, he has no means of answering these questions. When he reads the publications of other ecologists he is in even more of a quandary, and constantly finds himself asking, "If I had been there, would I have come to the same conclusion?" To resolve these doubts, methods are required that do not depend at any stage upon subjective judgment. If such methods were in general use, as they are in most other sciences, it would be easy for the ecologist to check both the consistency of his work and its agreement with the work of others. He could still use visual impressions for work-a-day purposes, but in any critical work, and as a regular check on the results to which his visual impressions were leading, he would be able to fall back on these objective methods—rather as a good chemical laboratory keeps a set of accurately standardized weights, not for routine use, but for regularly checking those used every day.

For the objective description and classification of vegetation, the first requirement is detailed data from a representative set of samples. At the outset, it is usually necessary to impose restrictions on the sampling. These restrictions may be geographical, sampling being confined to a particular area, whether natural or arbitrary; they may depend on habitat conditions, as, for instance, when communities of epiphytes or aquatic plants are under study; they may even, for some purposes, depend on the vegetation itself, as when variations in the ground flora of beech-woods are being investigated. Whatever they may be, these restrictions should be made explicit, and it will be clear that the resulting classification will relate only to the vegetation thus restricted; for instance, if sampling is deliberately confined to rock clefts, the vegetational categories found may not be applicable in any way to the vegetation of rock faces, even though many of the same species may occur there. Within the framework of restrictions specified, sample areas should be distributed at random or in accordance with some scheme of restricted randomization. If, instead, the sample areas are selected, the requirement of objectivity is broken at the outset, and any resulting classification will classify not the vegetation but the particular areas chosen and will reflect any subconscious bias in their selection.

Even where data have been derived from random quadrats, there is still abundant scope for subjective influence in their grouping into classes. Given the basis of classification—whether presence of species, dominance, habitat features, or structure (and there seems, as yet, to be no satisfactory basis for deciding among the various schools of thought on this matter)—one has still to determine what ranges of the characteristics used shall be regarded as indicating membership of this or that vegetation category and how data regarding the various features should be combined. For those ecologists who have been content to depend on the dominant species only for defining the class of vegetation the use of objective criteria has been relatively simple. But classifications based on dominance have often been regarded as unsatisfactory. Communities defined on the dominant species of the highest stratum only are apt to be too broad for general use; if they are defined on a combination of dominants in each stratum, the vegetation is often divided into a large number of inconveniently small units (cf. Ashby's (1935, 1936) comments on the Uppsala methods of classifying vegetation). Moreover, within an area dominated by one species there may be enclaves in which the vegetation differs from that of the rest of the area only in the absence of this dominant species and in nothing else. Consequently, many ecologists prefer a more flexible system in which several alternative criteria are available, supplementing one another in determining the class membership of a particular quadrat. The doctrine of "characteristic species" introduced by Gradmann (1909) and developed by Braun-Blanquet (1921, 1928) is such a system. A group of species is found that occur only or preferentially in a certain type of plant community, and their presence in a quadrat is then taken as indicating that it is to be allocated to that community. This procedure is potentially fully objective. But, in practice, not only do Braun-Blanquet and his school select their areas for detailed study but their determination of characteristic species is also far from objective—either being based on general previous experience or on inspection of the species lists from the various stands. In order to apply consistently such complex criteria of classification, not only is random collection of quadrat data called for but an objective method is necessary for dealing with the data after collection.

It is the purpose of the present series of papers to introduce some objective methods lending themselves to statistical control which may be used for the classification of quadrat data, and to illustrate their application. Though floristic criteria will mainly be used, some of the methods could equally appropriately be applied to classification by ecological factors or by groups of species related in biology or in geographical distribution, as suggested by Schmid (1942, 1944, 1950). It must be understood, however, that the classifications arrived at by the methods proposed will reflect the true vegetational relationships only if the quadrats have been placed by appropriate randomization techniques.

II. Interspecific Correlation as an Index of Heterogeneity

The vegetation of an area may be regarded as heterogeneous if, in at least one species, the distribution of individuals, or of groups of individuals behaving in distribution as a unit, is patchy. The most usual cause of heterogeneity in this sense is that the habitat factors in one part of the area are more favourable to the growth of the species than elsewhere. Now, it is unlikely that variations in habitat factors will affect the distribution of one species only; if one species is non-randomly distributed, then it is highly likely that others will also show non-random distribution, and that they will either tend to be abundant in the same areas as the first species or to avoid those areas. If the former, the quantities of the two species present in different quadrats will be positively correlated, if the latter, negatively correlated. Interspecific correlations may also arise when one species creates conditions favourable or unfavourable to the growth of another, the habitat conditions for the second species thus being rendered non-uniform. Consequently, if inspection of a set of quadrat data shows that the quantities of two species in the quadrats are correlated, it is probable that the distribution of one or both of these species over the area is non-uniform and that the habitat factors controlling them are also non-uniform. This applies, of course, to determinations of the simple presence or absence of a species in a quadrat just as much as to measurements of quantity. Tuomikoski (1942) was the first to treat interspecific correlation explicitly as an index of heterogeneity, although this had been suggested in the work of many previous investigators (e.g. Nordhagen 1928). Tuomikoski gave equal weight to positive and negative associations, but whether this is justified is somewhat doubtful (Goodall 1952). In any case, for the purpose of the present paper it is taken that only positive correlations between species provide evidence of heterogeneity.

This view of interspecific correlation as being fundamental to the separation of plant communities and to the recognition of vegetational heterogeneity which is a necessary prerequisite to it, is in line with much of the underlying theory of plant sociology. Many of the terms used, including "association" itself, reflect the fundamental place, often barely recognized, taken in the subject by interspecific correlation. It is accordingly held that subdivision of a group of quadrats is called for if the presence or quantities of the various species in the quadrats show positive correlation to a statistically significant degree. Given a set of quadrat data, one could determine whether they are uniform, coming from a single type of plant community, or whether on the other hand they are in need of subdivision, by studying the correlations among the species present. If the number of positive correlations among them exceeding a certain level of significance is greater than would be expected by chance once in 20 times (or whatever other limit is adopted), subdivision is called for.

If data only on the presence or absence of each species in each quadrat are to be used, the determination of correlations* may be greatly facilitated by the use of edge-punched cards. These have been extensively used by systematists, but their application to plant sociology appears to be new. If the records for each quadrat are entered on one such card and portions of the margin corresponding to the species recorded in it are cut away, the data may readily be sorted according to the presence of any given combination of species. Apart from facilitating determination of the number of quadrats containing particular pairs of species, these punched cards enable one readily to see which correlations are worth statistical test. If cards containing records of one species are separated and put at one end of the pile, and the pile is examined edgewise, it is often easy to notice that the cards in which a particular portion of the margin have been removed are proportionately more numerous in one than in the other series.

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* Some workers prefer the word "association" to express a relationship between variables which can take only two possible values. However, use of the word "association" in the present context would risk confusion with the unit of vegetational classification which goes by that name, so it seems preferable to use the term "correlation" in a broad sense to include such cases rather than restrict it to product-moment correlations.

The testing of homogeneity by computing product-moment correlations, where suitable data are available, would be an impossibly burdensome task—and indeed, the technique of product-moment correlation might not be suited to the extremely skew distribution often found. Quantitative data could, however, be used in testing for homogeneity by taking an arbitrary dividing line at (say) the mean for each species, preparing a 2 × 2 table, and thus finding whether occurrences of the two species in excess of their respective means were positively associated.

It should be noted that, in testing for homogeneity in this way, the ordinary criteria of significance cannot be applied to each correlation separately. If, say, 20 species are present, then the number of possible correlations between them is 190, and it is more than likely that several of them will individually show a probability less than 0.05. A rough test of significance may be based on the fact that, on average, only once in 20 such sets of data will a single correlation have a probability as small as $0.05/N$, where N is the number of correlations tested; if the most highly correlated pair of species gives a value for P less than this, the group may be regarded as heterogeneous. In this connection, it should be remembered that the data may be too limited to demonstrate correlations, even if they exist, between some pairs of species; this is particularly true where only presence or absence of species is considered. For instance, if in 100 quadrats one species has a frequency of 90 per cent. and another 10 per cent., the highest degree of correlation that can be attained by the two species (when the second occurs only in the presence of the first) has a probability of 0.33. Any pairs of species which in this way cannot show correlation at the significance level under consideration should not, of course, be included in the number of possible correlations N. If no single correlation passes the significance level $P = 0.05/N$ but several approach it, another rough test may be applied. The number a passing another, less rigorous, level (say, $P = 0.01$) may be determined, and the sum of the a^{th} and subsequent terms in the binomial expansion

$$(0.99 + 0.01)^{N'},$$

where N' is the number of pairs of species the correlation between which could attain the significance level $P = 0.01$, may be taken as indicating approximately the joint probability of these correlations. If all the correlations tested were independent, this test would be precise; but in fact they are inter-linked, and an exact determination of the joint probability of any particular group of correlations found would be a formidable piece of computation.

III. Criteria for the Separation of Groups in a Heterogeneous Collection of Quadrats

Once it has been established that a particular collection of quadrats is heterogeneous, it is necessary to attempt to subdivide the collection into groups that will be internally homogeneous. Where only the presence or absence of each species is considered, this may be done in several ways. If two species have been shown to be positively correlated, this indication of heterogeneity may be eliminated from the subdivisions of the collection by taking as a potentially homogeneous group (1) all quadrats containing one of the two species; (2) all those *not* containing one of the two species; (3) all those quadrats containing both the species; or (4) those quadrats containing *neither* of the two species.* All these methods are illustrated in subsequent pages.

The purpose of the classification procedure is, of course, not simply to divide the collection of quadrats into groups showing no internal correlations between species, but into as *few* and as *large* such groups as possible. To this end it is suggested that in choosing interspecific correlations for elimination that correlation should be selected whose elimination will give the largest group of quadrats. Thus, if criterion (1) is being used, the most frequent species showing interspecific correlations will be chosen; if criterion (3), then the pair of species with the highest number of *joint* occurrences will be first used.

In determining the significance of correlations to decide which species to select or eliminate under criteria (1) and (2), it is necessary to have regard to the number of correlations tested. If 21 species have been recorded, then each is likely by pure chance to show one correlation "significant" at the 5 per cent. level. Therefore, a stiffer test of significance is required—in this hypothetical case, one correlation would need to have a value of $P < 0.0025$, or four correlations with the same species would need to have $P < 0.05$, before that species qualified as a basis for selection of quadrats.

The elimination of one such interspecific correlation will not in general exhaust the interspecific correlations in the group, though more than that one will often be eliminated (species are commonly correlated in groups of more than two). On the group of quadrats thus extracted from the whole collection, therefore, the same procedure will need to be repeated if it is found that this group is heterogeneous, and the process will continue until a group of quadrats homogeneous by the criteria of Section II has been extracted. The whole residue of quadrats apart from this homogeneous group may then be recombined and the process repeated. In this way a number of groups of quadrats, each internally homogeneous, may be extracted from the collection and a residue left containing no further significant correlations.

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* In this way the correlation is "channelled," so to speak, into the comparisons between quadrats in *different* groups, and is not shown between quadrats in the *same* group. Let us suppose that under method (1) a group containing species *A* has been separated on account of its correlation with species *B*. Within this group, any quadrats found to contain species *B* must necessarily also contain species *A*. But since the latter is present in *all* quadrats of the group, the correlation between the two species is indeterminate and non-significant. When consideration is extended from this one group to all groups, the correlation between the two species remains, of course, as high as ever.

When this has been done the next stage in the process begins. As has been said, the purpose of the classsification is to obtain the smallest possible number of homogeneous groups of quadrats. Therefore it is necessary, with the various groups of quadrats that have been extracted, to test whether they may be combined without the reappearance of interspecific correlations. The groups into which the quadrats were originally divided are thus recombined in successive stages until further combination cannot but lead to significant interspecific correlations and hence to heterogeneous groups.

The rest of this paper will be devoted to illustrations of the use of these methods for classification of quadrat data, only the presence of a species in a quadrat being considered and not the quantity in which it occurs. This is analogous to the methods of classifying vegetation developed by the Zürich-Montpellier school of plant sociologists, and particularly by Braun-Blanquet (1921, 1928). Though the quantities of the various species present in a stand are recorded in the form of rough visual estimates and some note is taken of the structure of the community, main attention is directed to the presence of an inter-correlated group of "characteristic" species, irrespective of the quantity in which they occur, and to the absence of species ascribed to other inter-correlated groups "characteristic" of other communities.

The procedures described in Section IV are somewhat arbitrary, and it is quite conceivable that other procedures would lead to similar results, perhaps with the expenditure of less effort. The end is here more than the means—provided the purpose of classifying the quadrats into internally homogeneous groups is attained, the procedure for attaining it is more a matter of convenience than of principle.

The same procedures could clearly not be applied without modification if the quantities of the various species in a quadrat were to be taken into account. In this event, there is no certain way of eliminating correlations from any subdivision of the collection. Selection of those quadrats in which the quantity of a species exceeds or falls below some arbitrarily chosen level will often render non-significant within the selected group any correlations in which that species was involved; but the evident artificiality of this procedure emphasizes the artificiality of classification in general as applied to vegetation. Where the features on which one classifies the vegetation vary continuously, any dividing line that one draws is bound to be arbitrary and the groups on either side of it will be artificial—though often practically useful.

IV. AN ILLUSTRATION

(*a*) *Source of the Data*

The data used in illustration of these methods were collected in the Victorian Mallee in December 1950. The vegetation of the area studied falls roughly into the "stunted mallee" category of Zimmer (1946) and would probably all be included by Wood (1937) and Beadle (1948) in the *Eucalyptus oleosa-E. dumosa* association — though, as will be seen, it is far from homogeneous. The topography is monotonous, sandy ridges running east and west, up to 10 m. high, being separated by hollows with heavier soil. *Eucalyptus* species are dominant over the whole area, *E. oleosa* being most important in the hollows and *E. dumosa* on the ridges; their heights range from 2 to 3 m. These mallees do not form a closed canopy, the average cover by all *Eucalyptus* spp. being about 50 per cent. The vegetation of hollows and ridges is most strikingly differentiated by the presence on the ridges of *Triodia irritans*, a grass forming large circular or annular tussocks, whose inflorescences reach a height of 1.5 m. In the hollows the ground is usually bare of herbaceous vegetation, except for scattered chenopods. According to local residents the area has never been grazed, cut, or cleared, and has not been burnt for many years; in fact, it carries practically virgin vegetation.

The area for study was delimited by reference to the point 35° S., 142° E., conveniently marked by a track intersection. A point 140 m. north-west of this intersection was taken as the south-east corner of an area 640 m. square, which was divided into 64 square plots within each of which four quadrats 5 m. square were placed by a restricted randomization. This quadrat size was considerably larger than the mean size of individuals or clumps of any of the species present. A chart was drawn of each quadrat indicating the ground covered by each individual tree, shrub, and tussock of *T. irritans*. For other angiosperm species, the number of individuals and an estimate of projective cover were recorded.

In the subsequent sections only data on presence or absence of each species in the quadrats have been used. The significance of correlations between the presence of two species was tested by preparing a 2 × 2 table and either calculating χ^2 (corrected for continuity) or determining the exact probability of the figures obtained, as described by Fisher (1937); the exact probability was in any case determined if the value for χ^2 was close to the significance level required.

(*b*) *Presence of a Single Correlated Species as Criterion for Selection (Procedure I)*

(i) *Separation of Groups.*—Fifty-eight species in all were distinguished on the 256 quadrats, but of these 27 occurred in no more than four quadrats, and so were neglected in the studies of correlation. Many of the interspecific correlations reached high levels of significance. In the 2 × 2 tables no fewer than 30 of the χ^2 values exceeded 20.0, and one reached 102.11. There was thus no doubt as to the heterogeneity of the collection. *Eucalyptus dumosa* was the most frequent species, occurring in 170 quadrats, and was significantly correlated with a number of others, for instance with *Triodia irritans* ($\chi^2 = 58.48$). The first step was thus the extraction of those quadrats containing *E. dumosa.*

Within the 170 quadrats containing *E. dumosa* highly significant positive correlations continued to appear between species, for instance between *T. irritans* and *Melaleuca uncinata* ($\chi^2 = 18.07$). *T. irritans* was the most frequent species in this group, so the second step was the extraction of quadrats containing *T. irritans* as well as *E. dumosa.*

The 119 quadrats remaining in this selected group were still heterogeneous. *Stipa variabilis* and *Vittadinia triloba,* for instance, gave a χ^2 value of 23.25. The most frequent species in this group (apart from the two by which it was defined) was *Dodonaea bursariifolia,* but this showed no correlations with any other species reaching a significance greater than corresponded to $P = 0.01$. The second most abundant species was *S. variabilis.* Accordingly the next step in selection was based on this species.

Within the 53 quadrats containing *E. dumosa, T. irritans,* and *S. variabilis* none of the interspecific correlations had a probability less than 0.01. Accordingly, this group was considered as homogeneous and was set aside without further subdivision; it will be referred to as **group A.** The residue of 203 quadrats remaining after extraction of group A was still highly heterogeneous. The value of χ^2 for the relationship between *Eucalyptus oleosa* and *Bassia uniflora,* for instance, was 55.43. *E. oleosa* being the most frequent species in this residue, the next step was to separate from it the 121 quadrats containing this species. Within this subgroup highly significant correlations were again frequent, for instance, that between *B. uniflora* and *Zygophyllum apiculatum* ($\chi^2 = 12.79$). *B. uniflora* being the most frequent species (apart from *E. oleosa*) in this subgroup, the 92 quadrats containing this species formed the next selection.

These 92 quadrats containing both *E. oleosa* and *B. uniflora,* after elimination of group A, were still not fully homogeneous. A highly significant correlation existed within it between *Cassia eremophila* and *Westringia rigida* ($\chi^2 = 44.43$). Although *C. eremophila* was not the most abundant species within this group (apart from the two defining species), none of the more abundant species showed any significant correlations with others; accordingly, selection was based on the presence of *C. eremophila* and gave a group of 17 quadrats. Within these 17 quadrats, no further significant correlations were to be found; accordingly, these formed the second homogeneous group, which will be termed **group B.**

The residue of 186 quadrats remaining after elimination of groups A and B was still heterogeneous. The most frequent species, *E. dumosa,* still showed correlations with a number of others, for example, with *D. bursariifolia* ($\chi^2 = 25.70$). Within the 115 quadrats containing *E. dumosa* there were also significant relationships, for instance between *T. irritans* (the most abundant species after *E. dumosa*) and *D. bursariifolia* ($\chi^2 = 13.75$). Within the group of 66 quadrats defined by the presence of both *E. dumosa* and *T. irritans* after the elimination of groups A and B there were no longer any significant correlations; accordingly this became our homogeneous **group C.**

The residue of 120 quadrats, after elimination of group C, continued to show significant correlations, for instance between *T. irritans* and *M. uncinata* ($\chi^2 = 23.19$). The most frequent species in this group was *B. uniflora*, the highest correlation shown by *B. uniflora* with any other species being that with *E. oleosa* ($\chi^2 = 9.60$). This degree of correlation, while it would not, in itself, have provided satisfactory evidence of heterogeneity in the group, was sufficient to show that *B. uniflora* shared in this heterogeneity (for, since the number of species with which *B. uniflora* could give such a high χ^2 was only six, a higher value would occur by chance less than once in 100 such sets of observations); consequently *B. uniflora* defined the next group to be selected. Within this group of 90 quadrats only two interspecific correlations were found to exceed the value of χ^2 corresponding to a probability of 1 per cent. Since the number of pairs of species tested was 75 this could not be regarded as evidence of heterogeneity. Accordingly these 90 quadrats became **group D.**

The 30 quadrats still unallocated showed no interspecific correlations reaching a high significance level; thus, without further separation, they could be designated as **group E.**

(ii) *Recombination.*—The 256 quadrats had thus been divided into five groups, each of which was internally homogeneous as judged by interspecific correlations. The question now arose: was this number of groups a minimum which could not be further reduced? In order to test this it was necessary to bring these five groups together in their various possible combinations, and to find whether recombining them caused significant interspecific correlations to emerge again.

First the final residue, group E, was considered in its possible combinations with the other groups. It had already been shown that the larger group formed by combining groups D and E was heterogeneous (see above). If groups E and C were combined, two correlations reached a high significance level (*S. variabilis* and *V. triloba*, $P = 0.00071$; *W. rigida* and *Myoporum platycarpum*, $P = 0.00068$); since the correlations could reach the 0.1 per cent. significance level only in 76 pairs of species, these two correlations taken together indicated a high degree of heterogeneity. Likewise, group E could not be combined with group B (for instance, for *B. uniflora* and *C. eremophila* $\chi^2 = 38.92$). On the other hand, when groups A and E were combined the resulting 83 quadrats showed no significant interspecific correlations.

Since it had been established in this way that it was possible to combine groups A and E and thus reduce the total number of groups to four, the next step was to test whether this combined group could be further combined with one of the remaining three groups; but when groups B, C, and D were combined in turn with (A + E), significant correlations appeared in every case.

For instance, correlations occurred in:

Group B + (A + E) between *B. uniflora* and *C. eremophila* ($\chi^2 = 28.98$);
Group C + (A + E) between *S. variabilis* and *V. triloba* ($\chi^2 = 29.99$);
Group D + (A + E) between *M. uncinata* and *T. irritans* ($\chi^2 = 35.47$).

It was likewise found that groups B, C, and D could not be combined with one another. For instance, the following correlations became significant:

in group B + C, between *B. uniflora* and *C. eremophila* ($\chi^2 = 62.23$);
in group B + D, between *W. rigida* and *C. eremophila* ($\chi^2 = 45.72$);
in group C + D, between *B. uniflora* and *E. oleosa* ($\chi^2 = 75.08$).

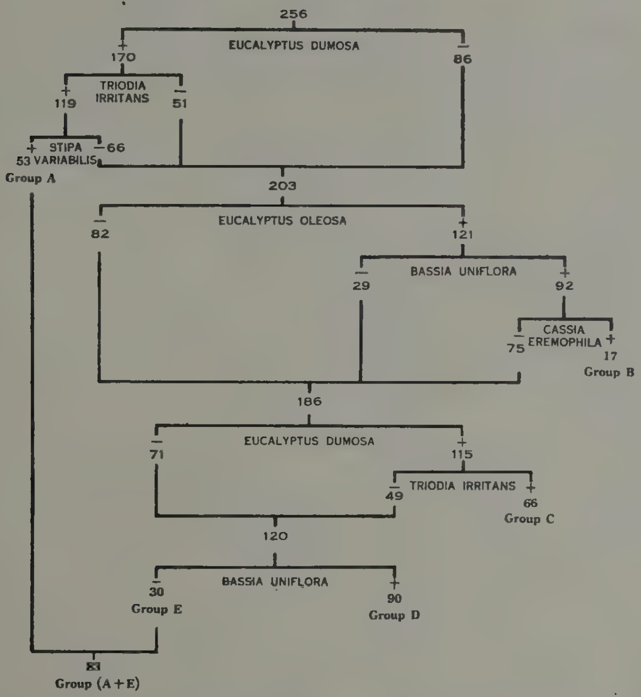
256
EUCALYPTUS DUMOSA
+ 170
− 86
TRIODIA IRRITANS
+ 119
− 51
+ STIPA VARIABILIS 53
−66
Group A
203
EUCALYPTUS OLEOSA
− 82
+ 121
BASSIA UNIFLORA
− 29
+ 92
CASSIA EREMOPHILA
− 75
+ 17
Group B
186
EUCALYPTUS DUMOSA
− 71
+ 115
TRIODIA IRRITANS
− 49
+ 66
Group C
120
BASSIA UNIFLORA
− 30
Group E
+ 90
Group D
83
Group (A + E)

Fig. 1.—Stages in the separation and recombination of groups by procedure I. At each stage the number of quadrats in which the species in question is present (+) and absent (—) is indicated.

Thus, there had been separated from the original 256 quadrats groups of 90, 83, 66, and 17 quadrats, each of which was internally homogeneous by the criterion adopted, but which all appeared to be distinct in that no two could be combined without creating heterogeneity within the group. The successive stages in the procedure are illustrated diagrammatically in Figure 1, and the results of classification are presented in Table 1, where the frequency in each group of quadrats is shown for every species occurring in at least five quadrats in all.

TABLE 1

FREQUENCY (PER CENT.) OF SPECIES IN FOUR GROUPS OF QUADRATS BASED ON PRESENCE OF SINGLE SPECIES SHOWING POSITIVE CORRELATIONS

Frequencies of 50 per cent. or more have been given in bold type

Species	Group			
	A+E	B	C	D
	No. of quadrats			
	83	17	66	90
Acacia rigens A. Cunn.	2	0	5	0
Bassia parviflora Anders	2	0	0	4
B. uniflora R. Br.	17	**100**	5	**100**
Beyeria opaca F. Muell.	1	6	5	0
Callitris verrucosa R. Br.	1	0	26	0
Cassia eremophila A. Cunn.	1	**100**	0	2
*Chenopodium pseudomicrophyllum** (1)	5	6	2	22
*C. pseudomicrophyllum** (2)	12	6	0	13
Danthonia semiannularis R. Br.	20	0	6	7
Dodonaea bursariifolia Behr	**53**	0	**71**	17
D. stenozyga F. Muell.	1	0	0	6
Enchylaena tomentosa R. Br.	4	24	0	3
Eucalyptus calycogona Turcz.	14	18	11	30
E. dumosa† A. Cunn.	**81**	**12**	**100**	39
E. oleosa F. Muell.	49	**100**	24	**81**
Grevillea huegelii Meiss	5	35	8	4
Kochia pentatropis R. Tate	2	24	0	7
Lepidosperma viscidum R. Br.	1	0	9	0
Lomandra leucocephala R. Br.	4	0	8	0
Melaleuca pubescens Schau.	4	0	8	0
M. uncinata R. Br.	**55**	0	**53**	3
Micromyrtus ciliatus J. M. Black	0	0	9	0
Myoporum platycarpum R. Br.	2	0	5	0
Olearia muelleri Bth.	5	**59**	0	6
Santalum murrayanum F. Muell.	1	12	5	1
Stipa elegantissima Lab.	1	12	0	3
S. mollis R. Br.	7	0	5	10
S. variabilis Hughes	**87**	**88**	0	**78**
Triodia irritans R. Br.	**78**	6	**100**	3
Vittadinia triloba D.C.	46	24	11	37
Westringia rigida R. Br.	6	**71**	5	3
Zygophyllum apiculatum F. Muell.	4	**65**	2	47

* *C. pseudomicrophyllum* Aellen occurs in this area in two forms which in due course will probably receive taxonomic recognition as distinct varieties or even species. They are readily distinguishable in the field, being respectively prostrate and erect in habit; form (2) also seems to lose its leaves much more readily than (1). As the data here show, their sociological affinities seem to be distinct, and the records have accordingly been kept separate.

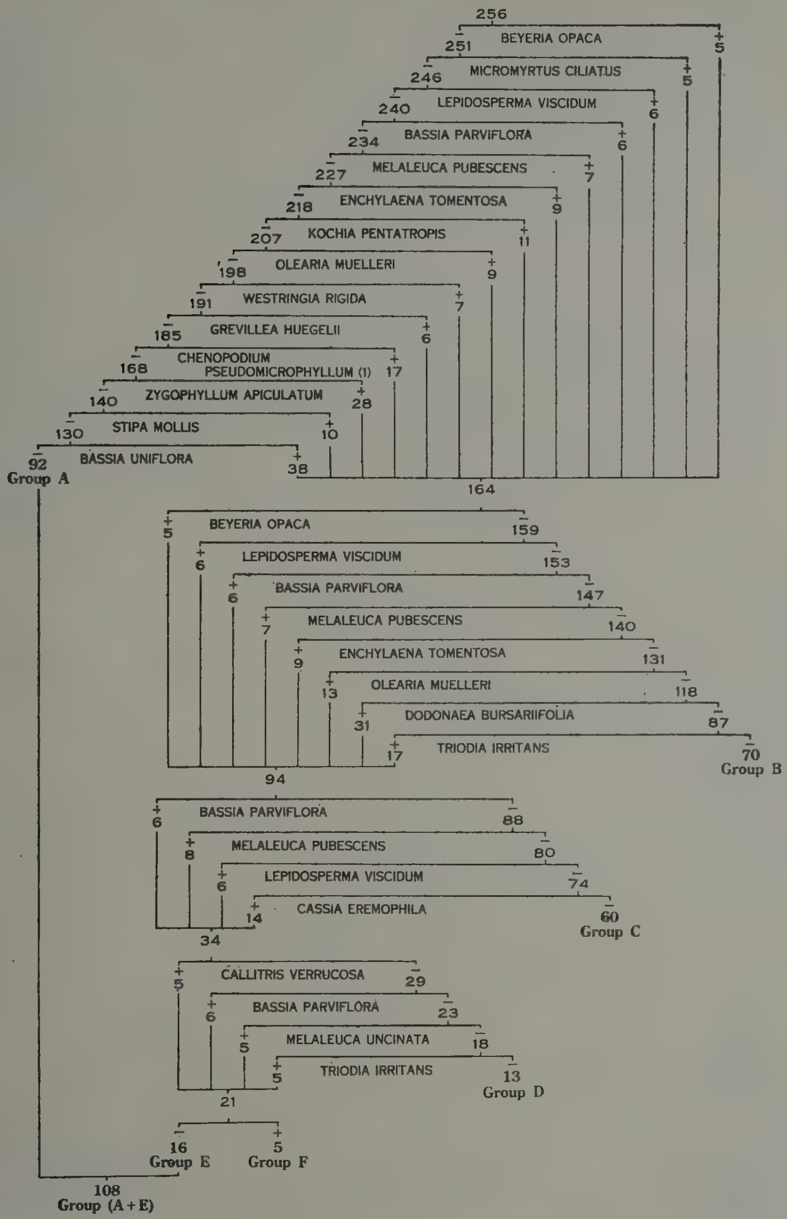
256
251
BEYERIA OPACA
+5
246
MICROMYRTUS CILIATUS
+5
240
LEPIDOSPERMA VISCIDUM
+6
234
BASSIA PARVIFLORA
+6
227
MELALEUCA PUBESCENS
+7
218
ENCHYLAENA TOMENTOSA
+9
207
KOCHIA PENTATROPIS
+11
198
OLEARIA MUELLERI
+9
191
WESTRINGIA RIGIDA
+7
185
GREVILLEA HUEGELII
+6
168
CHENOPODIUM PSEUDOMICROPHYLLUM (1)
+17
140
ZYGOPHYLLUM APICULATUM
+28
130
STIPA MOLLIS
+10
92
Group A
BASSIA UNIFLORA
+38
164
+5
BEYERIA OPACA
159
+6
LEPIDOSPERMA VISCIDUM
153
+6
BASSIA PARVIFLORA
147
+7
MELALEUCA PUBESCENS
140
+9
ENCHYLAENA TOMENTOSA
131
+13
OLEARIA MUELLERI
118
+31
DODONAEA BURSARIIFOLIA
87
+17
TRIODIA IRRITANS
70
Group B
94
+6
BASSIA PARVIFLORA
88
+8
MELALEUCA PUBESCENS
80
+6
LEPIDOSPERMA VISCIDUM
74
+14
CASSIA EREMOPHILA
60
Group C
34
+5
CALLITRIS VERRUCOSA
29
+6
BASSIA PARVIFLORA
23
+5
MELALEUCA UNCINATA
18
+5
TRIODIA IRRITANS
13
Group D
21
16
Group E
+5
Group F
108
Group (A+E)

Fig. 2.—Stages in the separation and recombination of groups by procedure II.

† *E. dumosa* and *E. oleosa* var. *glauca* occur together in this area, and appear to be indistinguishable in the vegetative state (at the time of observation, two-thirds of these plants were without flower-buds or fruit). They have accordingly been combined under the former name.

(*c*) *Absence of a Single Correlated Species as Criterion for Selection* (*Procedure II*)

Interspecific correlations could be eliminated as well by excluding all quadrats in which one of the associated species occurred as by excluding those in

Table 2

FREQUENCY (PER CENT.) OF SPECIES IN FIVE GROUPS OF QUADRATS BASED ON ABSENCE OF SINGLE SPECIES SHOWING POSITIVE CORRELATIONS

Species	Group				
	A+E	B	C	D	F
	No of quadrats				
	108	70	60	13	5
Acacia rigens	2	0	5	0	0
Bassia parviflora	1	0	0	0	**100**
B. uniflora	2	**99**	**62**	**93**	**80**
Beyeria opaca	1	0	5	8	0
Callitris verrucosa	11	0	10	0	0
Cassia eremophila	1	9	0	**100**	0
Chenopodium pseudomicrophyllum (1)	0	21	15	8	20
C. pseudomicrophyllum (2)	6	2	13	15	**100**
Danthonia semiannularis	15	6	8	8	20
Dodonaea bursariifolia	**65**	0	**57**	0	40
D. stenozyga	1	6	2	0	0
Enchylaena tomentosa	1	0	7	31	20
Eucalyptus calycogona	7	30	20	23	**100**
E. dumosa	**87**	27	**85**	23	**60**
E. oleosa	31	**81**	**65**	**93**	**100**
Grevillea huegelii	0	4	17	46	0
Kochia pentatropis	0	4	8	31	0
Lepidosperma viscidum	7	0	0	0	0
Lomandra leucocephala	6	0	3	0	0
Melaleuca pubescens	7	0	0	0	0
M. uncinata	**69**	2	12	0	20
Micromyrtus ciliatus	1	0	8	0	0
Myoporum platycarpum	2	0	3	8	0
Olearia muelleri	1	0	10	**93**	0
Santalum murrayanum	3	0	3	15	0
Stipa elegantissima	0	2	5	8	0
S. mollis	0	4	23	0	20
S. variabilis	43	**73**	**73**	**93**	**80**
Triodia irritans	**88**	0	**62**	0	**60**
Vittadinia triloba	21	33	48	31	**80**
Westringia rigida	2	4	12	**77**	20
Zygophyllum apiculatum	1	47	22	**69**	20

which it did not (procedure I). The results of proceeding by successive stages in this way are shown in Figure 2. Eliminating 14 species in succession, beginning with those occurring only in five quadrats, leads to the first homogeneous group; elimination of eight from the residue leads to the second; and three further repetitions of the process result in the division of the data into six groups in all. Two of these may be recombined, so five groups are obtained consisting respectively of 108, 70, 60, 13, and 5 quadrats. The frequencies of the more important species in each of these groups are shown in Table 2.

(*d*) *Presence of a Pair of Correlated Species as Criterion for Selection* (*Procedure III*)

The third method of progressive selection mentioned above is that in which a correlation is not the occasion for selecting or rejecting the whole of the quadrats containing one of the species in question but only for selecting those containing both. The results with this method are illustrated in Figure 3. Here the first and second groups are obtained by the selection of quadrats containing two pairs of species in each case, and six further groups are obtained by selection from the residue at each stage of quadrats containing a single pair of correlated species. Four of these groups could be recombined without the reappearance of heterogeneity, and another two could also be combined, the final result thus being four groups with 115, 101, 28, and 12 quadrats respectively. The frequencies of the various species in these groups are given in Table 3.

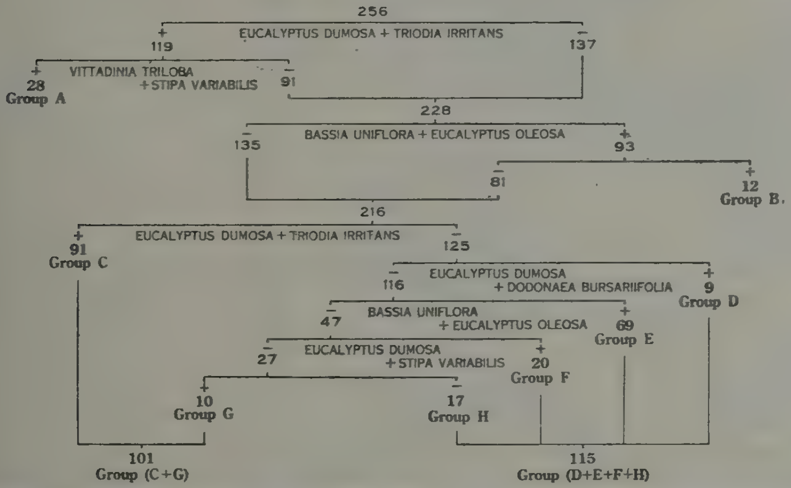
256
+
EUCALYPTUS DUMOSA + TRIODIA IRRITANS
−
119
137
+
VITTADINIA TRILOBA
+ STIPA VARIABILIS
−
28
Group A
91
228
−
BASSIA UNIFLORA + EUCALYPTUS OLEOSA
+
135
93
−
81
+
12
Group B
216
+
EUCALYPTUS DUMOSA + TRIODIA IRRITANS
−
91
Group C
125
−
116
EUCALYPTUS DUMOSA
+ DODONAEA BURSARIIFOLIA
+
9
Group D
−
47
BASSIA UNIFLORA
+ EUCALYPTUS OLEOSA
+
69
Group E
−
27
EUCALYPTUS DUMOSA
+ STIPA VARIABILIS
+
20
Group F
+
10
Group G
−
17
Group H
101
Group (C+G)
115
Group (D+E+F+H)

Fig. 3.—Stages in the separation and recombination of groups by procedure III.

(*e*) *Absence of a Pair of Correlated Species as Criterion for Selection* (*Procedure IV*)

The fourth and last of the criteria mentioned above for progressive selection of quadrats leading to a homogeneous group was the absence of both of a pair of correlated species. Once again, the procedure is presented in the form of a diagram (Fig. 4). The first homogeneous group required the elimination of

TABLE 3

FREQUENCY (PER CENT.) OF SPECIES IN FOUR GROUPS OF QUADRATS BASED ON JOINT PRESENCE OF PAIRS OF POSITIVELY CORRELATED SPECIES

Species	Group			
	A	B	C+G	D+E+F+H
	No. of quadrats			
	28	12	101	115
Acacia rigens	4	0	4	0
Bassia parviflora	7	0	0	3
B. uniflora	43	**100**	5	**83**
Beyeria opaca	0	9	4	0
Callitris verrucosa	0	0	18	0
Cassia eremophila	0	**100**	0	7
Chenopodium pseudomicrophyllum (1)	4	0	1	21
C. pseudomicrophyllum (2)	21	9	1	13
Danthonia semiannularis	18	0	12	9
Dodonaea bursariifolia	43	0	**71**	19
D. stenozyga	0	0	0	5
Enchylaena tomentosa	4	25	0	5
Eucalyptus calycogona	29	0	9	28
E. dumosa	**100**	9	**90**	44
E. oleosa	**57**	**100**	27	**80**
Grevillea huegelii	0	**50**	7	5
Kochia pentatropis	7	25	0	6
Lepidosperma viscidum	4	0	6	0
Lomandra leucocephala	0	0	8	0
Melaleuca pubescens	0	0	8	0
M. uncinata	32	0	**62**	10
Micromyrtus ciliatus	0	0	6	0
Myoporum platycarpum	0	0	3	2
Olearia muelleri	0	**75**	0	9
Santalum murrayanum	0	17	4	1
Stipa elegantissima	0	17	1	3
S. mollis	15	0	5	8
S. variabilis	**100**	**91**	30	**77**
Triodia irritans	**100**	9	**100**	4
Vittadinia triloba	**100**	9	8	39
Westringia rigida	11	**100**	3	4
Zygophyllum apiculatum	0	**67**	1	42

eight correlated pairs of species, the second seven, the third and fourth three each, and a single correlation separated the residue into two homogeneous groups, making six in all. Two pairs of these groups could be combined, the four final groups consisting of 102, 86, 42, and 26 quadrats. The frequencies of the species in each group are shown in Table 4.

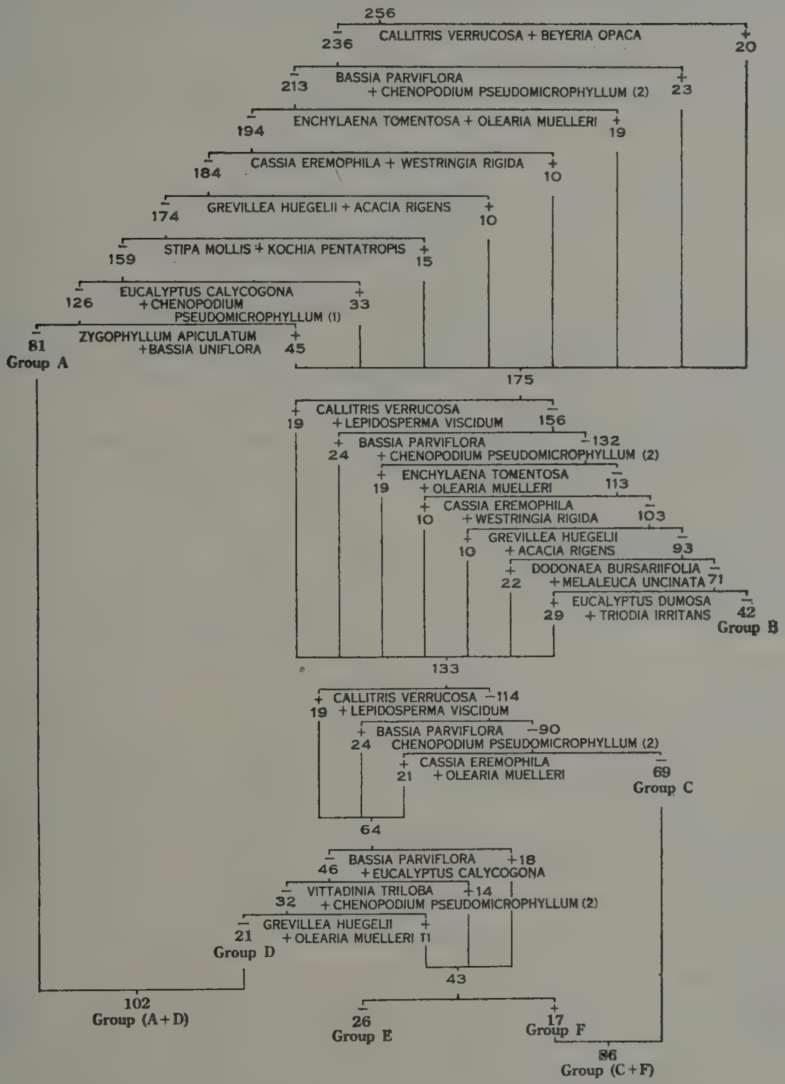
256
CALLITRIS VERRUCOSA + BEYERIA OPACA
− 236
+ 20
BASSIA PARVIFLORA + CHENOPODIUM PSEUDOMICROPHYLLUM (2)
− 213
+ 23
ENCHYLAENA TOMENTOSA + OLEARIA MUELLERI
− 194
+ 19
CASSIA EREMOPHILA + WESTRINGIA RIGIDA
− 184
+ 10
GREVILLEA HUEGELII + ACACIA RIGENS
− 174
+ 10
STIPA MOLLIS + KOCHIA PENTATROPIS
− 159
+ 15
EUCALYPTUS CALYCOGONA + CHENOPODIUM PSEUDOMICROPHYLLUM (1)
− 126
+ 33
ZYGOPHYLLUM APICULATUM + BASSIA UNIFLORA
− 81
Group A
+ 45
175
CALLITRIS VERRUCOSA + LEPIDOSPERMA VISCIDUM
+ 19
− 156
BASSIA PARVIFLORA + CHENOPODIUM PSEUDOMICROPHYLLUM (2)
+ 24
− 132
ENCHYLAENA TOMENTOSA + OLEARIA MUELLERI
+ 19
− 113
CASSIA EREMOPHILA + WESTRINGIA RIGIDA
+ 10
− 103
GREVILLEA HUEGELII + ACACIA RIGENS
+ 10
− 93
DODONAEA BURSARIIFOLIA + MELALEUCA UNCINATA
+ 22
− 71
EUCALYPTUS DUMOSA + TRIODIA IRRITANS
+ 29
− 42
Group B
133
CALLITRIS VERRUCOSA + LEPIDOSPERMA VISCIDUM
+ 19
− 114
BASSIA PARVIFLORA CHENOPODIUM PSEUDOMICROPHYLLUM (2)
+ 24
− 90
CASSIA EREMOPHILA + OLEARIA MUELLERI
+ 21
− 69
Group C
64
BASSIA PARVIFLORA + EUCALYPTUS CALYCOGONA
− 46
+ 18
VITTADINIA TRILOBA + CHENOPODIUM PSEUDOMICROPHYLLUM (2)
− 32
+ 14
GREVILLEA HUEGELII + OLEARIA MUELLERI
− 21
Group D
+ 11
43
− 26
Group E
+ 17
Group F
102
Group (A+D)
86
Group (C+F)

Fig. 4.—Stages in the separation and recombination of groups by procedure IV.

V. Discussion

Four different classifications of the same set of data having been derived by as many different procedures, the question whether these four classifications have much in common immediately arises. In fact, they have a good deal. Three of the four procedures divide the quadrats into four groups, and procedure II differs from the others only in creating a fifth very small group. If the groups derived by two procedures are compared, it is found that they can be matched in pairs, each group derived by one procedure corresponding with one derived by the other, and containing a large proportion of quadrats in common with it.

TABLE 4

FREQUENCY (PER CENT.) OF SPECIES IN FOUR GROUPS OF QUADRATS BASED ON JOINT ABSENCE OF PAIRS OF SPECIES SHOWING POSITIVE CORRELATIONS

Species	Group			
	A+D	B	C+F	E
	No. of quadrats			
	102	42	86	26
Acacia rigens	0	0	6	0
Bassia parviflora	0	0	4	8
B. uniflora	4	**98**	**68**	**81**
Beyeria opaca	3	0	1	4
Callitris verrucosa	17	0	1	0
Cassia eremophila	4	0	0	**62**
Chenopodium pseudomicrophyllum (1) ..	0	21	15	15
C. pseudomicrophyllum (2)	0	0	17	31
Danthonia semiannularis	16	7	8	4
Dodonaea bursariifolia	**67**	0	44	0
D. stenozyga	1	5	3	0
Enchylaena tomentosa	1	0	4	19
Eucalyptus calycogona	0	31	33	31
E. dumosa	**85**	0	**87**	31
E. oleosa	32	**88**	**64**	**89**
Grevillea huegelii	0	0	12	35
Kochia pentatropis	0	2	7	19
Lepidosperma viscidum	6	0	1	0
Lomandra leucocephala	7	0	1	0
Melaleuca pubescens	7	0	1	0
M. uncinata	**70**	0	13	8
Micromyrtus ciliatus	3	0	3	0
Myoporum platycarpum	2	0	2	4
Olearia muelleri	0	0	0	**73**
Santalum murrayanum	3	0	2	8
Stipa elegantissima	0	2	3	8
S. mollis	0	2	18	4
S. variabilis	41	**69**	**74**	**85**
Triodia irritans	**86**	0	**55**	0
Vittadinia triloba	18	29	**51**	8
Westringia rigida	3	0	8	**50**
Zygophyllum apiculatum	2	**52**	20	**62**

It is thus possible to equate the groups in the four classifications one with another, as shown in Table 5. The species name against each grouping is intended to serve merely as a means of convenient designation; the species is not held to have any special position in, or relation to, the grouping, though one with high constancy and fidelity within the limits of the study has been chosen in each case.

Within each grouping, a substantial "hard core" of quadrats is consistently allotted to that grouping by all four procedures. The numbers of such quadrats are:

Cassia eremophila grouping	9
Bassia uniflora grouping	40
Dodonaea bursariifolia grouping	45
Vittadinia triloba grouping	15

Thus 109 quadrats are similarly allotted by all four procedures. If, for each pair of procedures, the number of quadrats similarly allotted is determined, it is found that procedures I and III have most in common, 196 quadrats agreeing in their allocation. Procedures II and IV are almost as similar, the number of quadrats similarly grouped being here 194. On the other hand, procedures I and IV differ considerably more, and only 135 quadrats are allotted to the same groupings.

Table 5

EQUIVALENCE OF GROUPS DERIVED BY DIFFERENT PROCEDURES

Designation	Procedure			
	I	II	III	IV
Cassia eremophila grouping	B	D	B	E
Bassia uniflora grouping	D	B	D+E+F+H	B
Dodonaea bursariifolia grouping ..	C	A+E	C+G	A+D
Vittadinia triloba grouping	A+E	C	A	C+F

The small group F of procedure II has affinities with the *Bassia* and *Vittadinia* groupings.

There is little consistency, as between procedures, in the fate of the quadrats other than those of the "hard cores" of the four groupings. Examples of the relationships are presented in diagrammatic form in Figure 5*A*,*B* for the procedures giving best (I and III) and worst (I and IV) agreement. The shaded areas represent quadrats allotted to the same groupings by the two procedures, the unshaded portions those allotted to different groupings.

If a choice has to be made between these four procedures, none of which has any greater *a priori* justification than the others, the fact that procedure II has failed to reduce the quadrats to the smallest possible number of homogeneous groups tells strongly against it. The best criterion for choice among the four procedures is probably their success in achieving their declared aim —

separation of the data into homogeneous groups. Table 6 shows the number of interspecific correlations, within the final groups formed by each procedure, that pass three significance levels.

Table 6

SUCCESS OF DIFFERENT PROCEDURES IN DIVIDING DATA INTO HOMOGENEOUS GROUPS

	Number of Interspecific Correlations with P		
	$<0{\cdot}05$	$<0{\cdot}01$	$<0{\cdot}001$
Procedure I	3	2	0
Procedure II	6	3	1
Procedure III	7	7	2
Procedure IV	18	5	1

The degree of homogeneity, as judged by interspecific correlations, is clearly greatest in the groups resulting from procedure I. Moreover, procedure I is the easiest to apply; the numbers of successive eliminations and of recombinations tested are shown in Table 7. As will be seen from these figures, procedure I is more expeditious in subdividing the quadrat data than any of the others; it

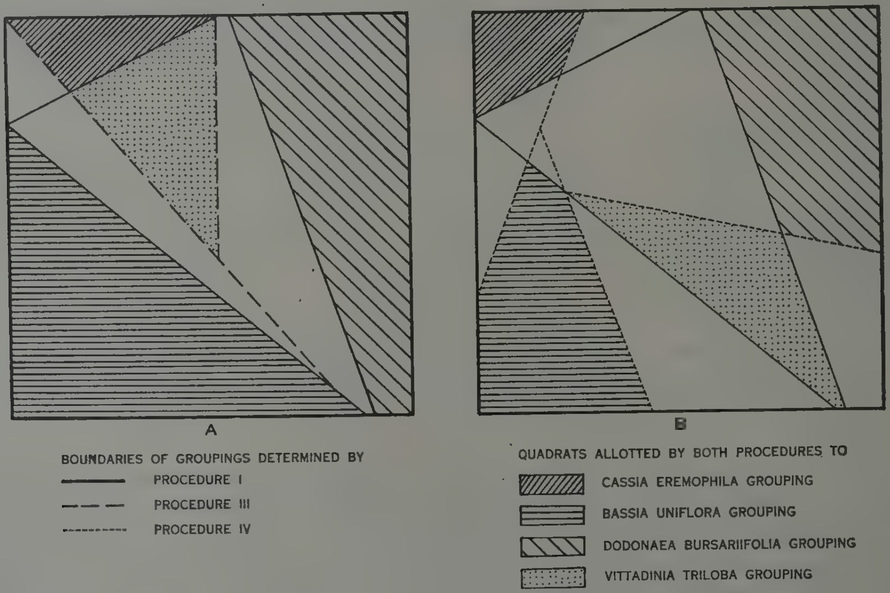
A
B
BOUNDARIES OF GROUPINGS DETERMINED BY
PROCEDURE I
PROCEDURE III
PROCEDURE IV
QUADRATS ALLOTTED BY BOTH PROCEDURES TO
CASSIA EREMOPHILA GROUPING
BASSIA UNIFLORA GROUPING
DODONAEA BURSARIIFOLIA GROUPING
VITTADINIA TRILOBA GROUPING

Fig. 5.—Comparison of results obtained with different procedures. The areas of the different portions of the diagrams represent the numbers of quadrants allotted to the various groups, and the shaded portions the numbers allotted similarly by both procedures. *A*, procedures I and III; *B*, procedures I and IV.

also gives a smaller number of groups in the first instance, thus requiring fewer tests of recombination. Thus not only does procedure I give more homogeneous groupings of quadrats than the other procedures but its greater simplicity and speed also may well be held to recommend it.

The reader may feel daunted by the amount of computational labour involved in the methods described here. In fact, they are not nearly as laborious as might appear at first glance. It has already been mentioned that the use of punched cards makes it possible to select by inspection species combinations that are likely to be significantly correlated, so that the number of correlations actually tested falls far short of the total number possible at any stage. In testing for heterogeneity a glance at the cards, together with previous knowledge based either on experience of the vegetation or earlier stages of the computational work, will often serve to reveal at least one highly significant correlation which is alone sufficient to make subdivision necessary or to preclude group recombination. In fact, in the present study the transcription of the data on to cards, their punching, and the whole of the computational work in procedure I were completed in five man-days of labour.

TABLE 7

ELIMINATIONS AND RECOMBINATIONS TESTED

	Eliminations	Recombinations
Procedure I	9	9
Procedure II	31	15
Procedure III	10	20
Procedure IV	22	14

As mentioned earlier, species with fewer than five occurrences in the group of quadrats under consideration were ignored in determining homogeneity. This practice was adopted for the sake of convenience only, and is not strictly justifiable; it could cause a distinct but uncommon community to be included with another commoner one. The groups resulting from procedure I were specially studied with this possibility in mind, but the correlations among species with less than five occurrences would not have caused the groups to be regarded as heterogeneous.

Though the presence and absence of different species show no significant positive correlations in the groups of quadrats separated, their quantities may still be correlated. To test this possibility, product-moment correlations were calculated between cover percentages for some of the more important species in each of the groups obtained by procedure I. Among the 25 correlations tested, two significant positive values were obtained—those between *E. dumosa* and *D. bursariifolia* in group A + E ($r = +0.346$, $n = 81$) and group D ($r = +0.314$, $n = 88$). These can hardly be accounted for satisfactorily by chance—the probability of two out of 25 values of P falling below 0.01 is about 0.03. The elimination of correlations between species, as judged by their presence or absence, has thus been partly but not wholly successful in eliminating also correlations in their quantities. If data on quantity had been used throughout, the final groupings would have been rather different.

Another question that will certainly arise in the reader's mind is whether there is any topographical relationship between quadrats allotted to the same grouping — whether quadrats of the same groupings are scattered higgeldy-piggeldy over the whole area, or whether they occur in compact blocks. The answer to this is contained in Figure 6, which shows the distribution over the

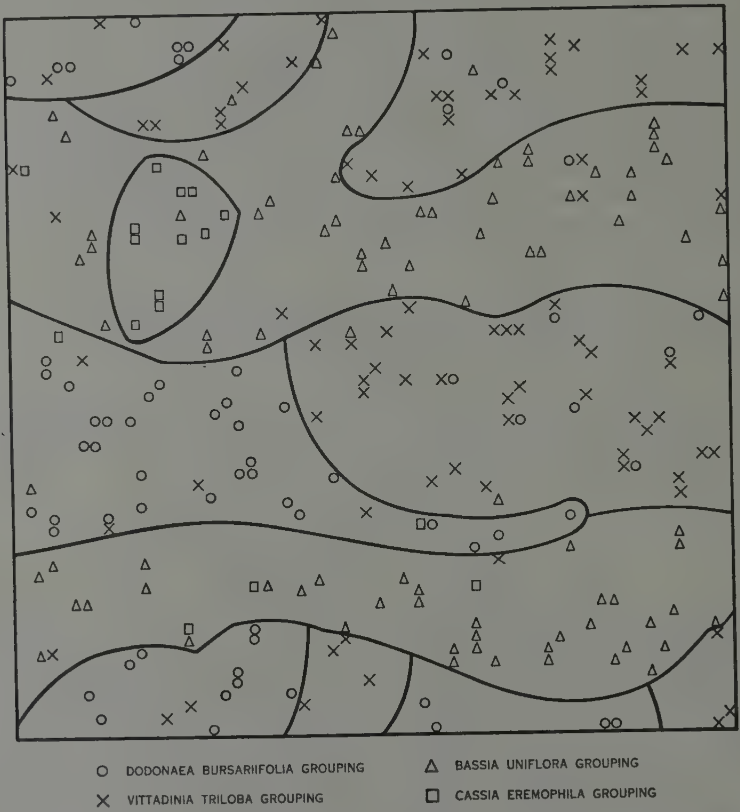
○ DODONAEA BURSARIIFOLIA GROUPING
△ BASSIA UNIFLORA GROUPING
✕ VITTADINIA TRILOBA GROUPING
□ CASSIA EREMOPHILA GROUPING

Fig. 6.—Plan of area studied, indicating position of each quadrat, and grouping as determined by procedure I.

area of quadrats allotted to the four groupings by procedure I. The area can be divided into a small number of portions in each of which the quadrats are almost all allotted to the same grouping. The group whose quadrats mingle most with those of others is group A + E, some of them occurring in regions predominantly occupied by group D, others in regions mainly containing group C; regions mainly occupied by group A + E also include several quadrats from each of these groups. On the other hand, there is little mingling of groups C and D. This suggests that group A + E (the *Vittadinia* grouping) is in some respects intermediate and transitional between groups C (*Dodonaea*) and D

(*Bassia*). Only one region is predominantly occupied by group B (*Cassia*) and this is surrounded by group D. The affinity between these two is further emphasized by the fact that the only aberrant quadrat within the former region belongs to group D, and most of the aberrant quadrats of group B are found in regions predominantly occupied by group D. The *Cassia* grouping may thus be perhaps regarded as a special type of the *Bassia* grouping. As might be expected from the general description of the vegetation given earlier, the outlines in Figure 6 reflect broadly the relief of the area. Three ridges run across the area from east to west, and these are the portions occupied in the main by the *Dodonaea* and *Vittadinia* groupings, while the valleys between contain the *Bassia* and *Cassia* groupings.

The methods described give no indication of the taxonomic status of the groupings extracted. The groupings will be elementary ones within the limits of analysis set by the area studied, the quadrat size, and the sampling intensity adopted, and will not be subject to further subdivision except in the light of further data; but objective methods do not tell one whether they should be regarded as associations, sub-associations, or some other unit in the vegetational hierarchy recognized by plant sociologists. The word "grouping" has therefore been adopted for the sake of its neutrality. Usage in different schools of plant sociology varies so widely in this respect, in spite of persistent efforts to attain uniformity, that discussion of the status of these "groupings" is hardly likely to be rewarding. It may be noted, however, that the definition of the association given by Horn af Rantzien (1951), "the unit of lowest rank which can be distinguished by the presence or absence of indicator species," comes close to describing the groupings of the present paper; this may be contrasted with the usage of Wood (1937) and Beadle (1948), for whom a single association would include all the vegetation described here and much more besides.

From time to time, ecologists have expressed doubts whether classification is an appropriate way of presenting the variations observed in vegetation (Ramenski 1930; Tuomikoski 1942; Schmid 1942, 1944, 1950; Whittaker 1951; Curtis and McIntosh 1951). It has been argued that the composition of vegetation could be represented in a multidimensional coordinate system, every feature measured in the vegetation (such as the proportion of a particular species) being allotted an axis. The vegetation of a particular sample area could then be represented by a point in the system, the coordinates of the point being given by the quantities of the various species present. Though these points would undoubtedly not be distributed evenly through the system, but rather would fall into clusters separated by regions of lower density, it is considered unlikely that their distribution would show the sharp boundaries implied by a classification system. Consequently, it is claimed that classification, though perhaps convenient, is an arbitrary and unnatural way of describing the variations in vegetation, and that methods should be sought in its place which would enable the variations to be treated as continuous. It is, of course, unlikely that such methods would ever completely displace classifications; classifications are usually easier to work with than coordinate systems, and it does little harm if boundaries are drawn between the clusters of points to separate distinct classes, so long as it is realized that this procedure is arbitrary and for practical convenience only.

But the greater convenience of classification does not absolve the scientist from seeking the true underlying relationships on which a systematic treatment of plant sociology should be based if it is claimed to be in any way natural.

Though this paper is concerned with classification, it must be emphasized that it is not intended to defend classification as a means of simplifying the diversity of vegetation. On the contrary, it feeds the fires of those who regard classification as inadequate. If vegetational patterns in the field fell into neat discrete classes, all procedures should give results agreeing much more closely than in fact they do. If the vegetation of an area were a mosaic of sharply distinguished "associations," each characterized by the presence of a different group of species, and the area were studied by quadrats small compared with the elements of the "mosaic" but large compared with that rather nebulous concept the "minimal area" of the association (see Goodall 1952), the four procedures would all yield the same groupings with the exception of the few quadrats straddling boundaries between associations. But in fact less than half the quadrats are similarly allotted by all procedures. This suggests that there are very large transition zones between areas covered by different associations, or, alternatively, that the vegetation forms in fact a varying continuum and that its subdivision into associations is purely artificial, serving human convenience perhaps, but reflecting only very crudely the relationships actually obtaining in nature. In a later paper in this series, it is hoped to present methods in which use is made of objective and statistical techniques for displaying the relationships between quadrat data without classification, vegetation being treated as a continuum rather than a conglomerate.

VI. ACKNOWLEDGMENTS

I am much indebted to Professor J. S. Turner for helpful criticism of this paper in draft. Some of the species collected were identified by Mr. E. J. Sonenberg, and all identifications were checked by Mr. J. H. Willis and Mr. R. V. Smith of the National Herbarium of Victoria. Mr. G. W. Davies gave much help in the computations and in the preparation of the diagrams.

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THE IDENTIFICATION OF THE SPOROMORPH *PHYLLOCLADIDITES* WITH *DACRYDIUM* AND ITS DISTRIBUTION IN SOUTHERN TERTIARY DEPOSITS

By Isabel C. Cookson[*]

[*Manuscript received June 18, 1952*]

Summary

The morphological similarity between the Tertiary sporotype *Phyllocladidites* and the pollen grains of the recent Tasmanian conifer *Dacrydium franklinii* is indicated.

It is suggested that, in future, pollen grains of this type should be referred to as *Dacrydiumites* and that the two sporomorphs already described should be known as *Dacrydiumites mawsonii*† and *Dacrydiumites ruei* respectively.

The Tertiary distribution of these sporomorphs is considered.

I. Introduction

In a previous article (Cookson 1947) a new sporotype *Phyllocladidites* was created for a distinctive type of coniferous pollen grain isolated from the Tertiary lignites of the Kerguelen Archipelago. This name was adopted on account of certain resemblances shown by it to the pollen of *Phyllocladus* and because it did not agree more exactly with any of the pollen descriptions of other conifers. Two sporomorphs, *P. mawsonii*† and *P. ruei,* were recognized and described. At that time it was suggested that *Phyllocladidites* might represent "pollen of extinct species of *Phyllocladus* or at least a member of the Phyllocladoideae."

It has since been found that this supposition was not correct and that the true affinity of "*Phyllocladidites*" is with the Tasmanian species of *Dacrydium, D. franklinii,* and not with *Phyllocladus.*

The facts supporting this taxonomic position and the changes in the nomenclature of the fossil pollen grains they involve will be considered here. Additional information concerning the geographical distribution of fossil pollen grains of the *Dacrydium franklinii* type will also be included.

II. Pollen Grains of Dacrydium franklinii Hook. f.

The description of the pollen grains of *Dacrydium franklinii* given by Erdtman in 1943 has been found adequate in all but one respect. In it no mention is made of one feature which has been both constant and conspicuous in the pollen samples studied. This is a localized and definitely circumscribed thickening of the exine situated between the proximal roots of the bladders and the thickened exine of the cap (Plate 1, Fig. 4). These thickenings, or "proximal tubercles" as they have been called in an earlier communication (Cookson 1947, pp. 132-3), are more or less circular in outline and their prominence is somewhat variable. In certain aspects of the grain they may be difficult to see but their occurrence has been so frequent that it seems doubtful whether they are ever entirely absent from normal pollen grains of this species. The tubercles develop at an early stage (Plate 1, Figs. 6-8) as minute outgrowths of the ektexine and gradually enlarge as the pollen grains mature.

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[*] Botany Department, University of Melbourne.

† By an etymological error, the final "*i*" was omitted from the original spelling (Cookson 1947).

In view of the regular occurrence of this morphological feature in pollen from male cones collected at two distinct localities in Tasmania the following amended description is given.

Description of Pollen Grains of D. franklinii (Plate 1, Figs. 1-8)

The body varies in shape according to the degree of expansion of the grain. It is oval to quadrangular in polar views of unexpanded grains with the width greater than or equal to the length; in fully expanded grains it is oval with the length greater than the width. Average measurements of fully expanded acetolysed grains are: width 29 μ (25-32 μ), length 33 μ (24-37 μ), overall length 56 μ (49-61 μ), and depth 28 μ (26-29 μ). The furrow is wide and slightly more convex than the cap and its membrane is thin and smooth.

The exine of the cap is distinctly two-layered, about 2.6-3 μ thick, and its surface has a finely granular texture. The bladders are small (19-27 μ long and 11-16 μ deep), strong, with a very small-meshed reticulum. A small tubercle, more or less circular in outline in surface view and of variable size, occurs between the proximal root of each bladder and the distal margin of the cap. These tubercles sometimes show the striated appearance that is evident in the exine of the cap.

This description is based upon the pollen grains from male cones collected during 1951 near Lake Vera on the route to Frenchman's Cap, Tasmania, and kindly forwarded by Dr. Winifred Curtis of Hobart, and at Corinna on the Pieman River, west coast of Tasmania, by Mr. T. E. Burns of Launceston.

III. Tertiary Pollen Grains of the Dacrydium franklinii Type

Comparison between the Tertiary pollen type *Phyllocladidites* and the pollen grains of *Dacrydium franklinii* show that the recent and fossil pollen grains have all their morphological features in common. Both types of grain are of medium size with a wide furrow, the bladders are small and firm with an indistinct reticulum, the exine of the cap is moderately thick, and the sculpture exceedingly fine; there is a small tubercle at the proximal root of each bladder.

Of these features the one possibly of the greatest diagnostic value is the development of proximal tubercles. These, as far as can be ascertained, only occur in the pollen of *Dacrydium franklinii* amongst living conifers and in those of *Phyllocladidites* amongst fossil species. This fact, especially when taken in conjunction with other morphological characters in common, provides overwhelming evidence that the fossil pollen type in question represents a species of *Dacrydium* closely related to *D. franklinii.* It should probably be mentioned at this point that the pollen morphology of *Dacrydium* is by no means uniform, several distinct and readily recognizable types occurring amongst its species (Cranwell 1941).

The identity of the sporotype *Phyllocladidites* with *Dacrydium* thus being established it naturally follows that its two sporomorphs should also be associated with that genus as *Dacrydiumites** *mawsonii* and *Dacrydiumites ruei* respectively. The original descriptions of these two forms are repeated here:

(*a*) *Dacrydiumites mawsonii* (Plate 1, Figs. 9-26)

Syn. *Phyllocladidities mawsonii* Cookson (1947).

"Grains circular, quadrangular or oval in polar view with the longer diameter in a plane either parallel to or across the furrow, 21-45 μ by 24-45 μ, average length about 30 μ and average width approximately 32 μ. Cap convex, faintly granular, furrow smooth, wide, clearly defined, and usually covered by the two small rather rigid wings that border it. Reticulations of air bladders poorly developed. Exine thick, 2.5-4 μ, proximal tubercles prominent."

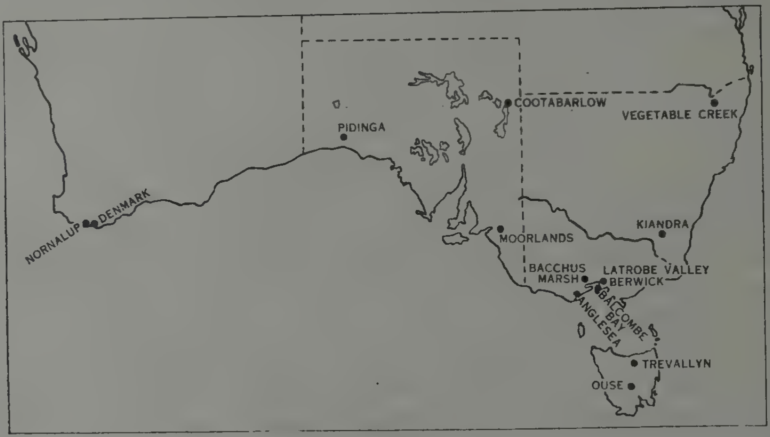

Fig. 1.—Southern Australia, showing location of deposits in which the sporomorph *Dacrydiumites mawsonii* has been found. (Prepared by the Geological Survey of Victoria.)

None of the examples of *D. mawsonii* from the type locality near Port Jeanne d'Arc, Kerguelen Archipelago (Plate 1, Figs. 24-26) was preserved in the fully expanded condition. The measurements given above are therefore not strictly comparable to those of fully expanded grains of *D. franklinii* recorded in Section II. Supplementary measurements, taken from fully expanded grains of *D. mawsonii* isolated from Australian Tertiary deposits, show that the dimensions of the living and fossil grains are of the same order. They are: body 29-37 μ long, 20-31 μ wide, 27-35 μ deep; overall length of grain 44-57 μ; bladders 16-27 μ long and 16-18 μ deep.

(*b*) *Dacrydiumites ruei* (Plate 1, Fig. 27)

Syn. *Phyllocladidites ruei* Cookson (1947)

"Expanded grains in polar view approximately circular, when unexpanded, completely folded or boat-shaped, 37-56 μ long by 34-50.5 μ wide with an average of 44 by 37 μ. Furrow wide, clear, partially bordered by two more or less well-developed frill-like air bladders. Exine of the furrow smooth, thin, that of the cap finely and closely granular, about 1.5-2 μ. Proximal tubercles usually well marked." *D. ruei* can be distinguished from *D. mawsonii* by its shallower, longer, and more frill-like bladders and thinner exine.

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* The ending "ites" signifies the fossil nature of the pollen grains (Erdtman 1947; Potonié, Thomson, and Thiergart 1950).

(*c*) *Distribution of* Dacrydiumites mawsonii *and* D. ruei

(i) *Dacrydiumites mawsonii*

(1) *Kerguelen Archipelago.*—Pollen grains of this type occur in the lignite and associated sandstone near Port Jeanne d'Arc and have been observed in residues from other exposures in the Archipelago.

(2) *Australia.*—Pollen grains morphologically similar to the sporomorph *D. mawsonii* occur more or less abundantly in Australian Early and Middle Tertiary carbonaceous sediments. These include deposits as far apart as south-western Western Australia (35° 00′ S., 133° 11′ E.) and north-eastern New South Wales (29° 27′ S., 151° 37′ E.), a distance of about 2070 miles. They have not been observed in the few samples from Queensland examined.

Some Australian examples are indistinguishable from acetolysed pollen grains of *D. franklinii;* others are somewhat divergent with rather more strongly developed tubercles and more prominently reticulated bladders. Allowing for such variations and the long time interval that has elapsed since the Early Tertiary period, it seems preferable that all should be associated with the fossil sporomorph *D. mawsonii,* rather than with the living species *D. franklinii.*

Western Australia.—Very little is known about the Tertiary flora of Western Australia. A few megascopic plant remains were described by Chapman and Crespin (1934) from Miocene beds at Cape Riche, but these provided no proof that the Tertiary temperate rain forests of eastern Australia extended to the western portion of the continent (Herbert 1950, p. 231). Some interest therefore attaches to the present record of the sporomorph *D. mawsonii* from three horizons in south-western Western Australia, where it occurs in small numbers with some of the pollen types already identified from eastern deposits. The latter will be considered in a later report.

Hay-Denmark Railway, deviation at 354 miles. Lignite from bores. Geol. Dept. Univ. W. Aust. No. 8662. Age: Tertiary. Sample 8662/1 50 ft. below surface, "coffee rock." Sample 8662/9 from No. 9 bore.

Nornalup Inlet. Lignite. Geol. Dept. Univ. W. Aust. No. 32982. Age: Tertiary.

South Australia.—The sporomorph *Dacrydiumites mawsonii* has occurred abundantly in three widely separated deposits in South Australia.

Pidinga. S.A. Dept. of Mines bore at 11-16 and 36-42 ft. Age: Tertiary.

Cootabarlow. East of Lake Frome. S.A. Dept. of Mines bore at 493-515 ft.; 515-537 ft.; and at 559-559.8 ft. Carbonaceous shale. Age: ? Early Tertiary.

Moorlands. Brown coal. Age: ? Oligocene.

Victoria.—Since *Dacrydiumites mawsonii* occurs in most of the Early Tertiary deposits of this State only the principal localities will be cited.

Eastern View (near Anglesea). Fine-grained carbonaceous sandstone from second-lowest of the five seams outcropping on beach between the Memorial Arch and the mouth of Spout Creek and from seam in Coal Mine Creek about 100 yd. upstream from road. Collected by A. B. Edwards and E. D. Gill. Age: Lower Eocene (Raggatt and Crespin 1950).

Latrobe Valley. At various horizons in the brown coal at Yallourn, in bore cores from Loy Yang and Maryvale, also in ligneous clays from the same area. Age: Oligocene.

Berwick. Sub-basaltic clay. Age: ? Oligocene. Nat. Mus. Vic. P. 15680.

Bacchus Marsh. Coal from Lucifer Mine. Age: Oligocene.

Anglesea. Carbonaceous sandstone. Age: Oligocene.

Balcombe Bay. Mudstone containing leaf remains. Age: Miocene.

New South Wales.—Kiandra, New Chum Hill. Low-grade coal. 70 ft. below basalt. Dulhunty sample 87. Age: ? Middle Eocene (Raggatt and Crespin 1952). Nat. Mus. Vic. P. 15711.

Vegetable Creek (Emmaville). Mudstone from deep leads. Age: ? Oligocene. Melb. Univ. Geol. Dept. No. 242.

Tasmania.—Ouse. Lignite seam in Ouse River about 400 yd. upstream from the Bridge Hotel. Age: ? Oligocene-Miocene.

Trevallyn. Investigation bores for the tailrace excavations for the Trevallyn Power Station. Pre-basaltic ligneous clay from bore 2009, 40-48 ft. Age: ? Oligocene-Miocene.

(3) *New Zealand.*—The probable presence of *D. mawsonii* in Lower Cretaceous to Upper Eocene beds was reported by R. A. Couper in 1951 but individual localities were not specified.

(ii) *Dacrydiumites ruei*

Kerguelen Archipelago.—This sporomorph is comparatively abundant in the lignite near Port Jeanne d'Arc and has been observed occasionally at other localities in the Archipelago.

Australia and Tasmania.—Pollen grains that could safely be associated with *D. ruei* have not been observed in samples either from the mainland or Tasmania.

New Zealand.—Couper (1951) reports that *D. ruei* is probably present in the Cretaceous and Eocene deposits of New Zealand.

IV. CONCLUSION

The extensive distribution of the sporomorph *Dacrydiumites mawsonii* in the southern hemisphere during the Early Tertiary period is in strong contrast to that of *Dacrydium franklinii*, its nearest ally in the present flora. This conifer is now confined to the western area of Tasmania whereas *D. mawsonii* must, at the least, have been widely spread in Tasmania, the southern half of Australia, New Zealand, and the islands of the Kerguelen Archipelago.

When, however, conclusions as to the past distribution of a particular species depend solely on similarity of pollen morphology, the possibility that its pollen grains might have been transported by prevailing winds from one station to another has to be considered. This seems especially necessary when the number of examples of a particular pollen type in a deposit is low.

Several instances of long-distance transport of pollen grains have been cited by Erdtman (1943), Faegri and Iversen (1950), and others. Quite recently Hafsten (1951) reported finding six pollen grains of *Nothofagus* in a peat profile at Tristan da Cunha. These, he assumed, had been "derived from *N. pumilio* forests in Tierra del Fuego and Patagonia" and carried by westerly winds across the south Atlantic Ocean to Tristan da Cunha, a distance of about 2800 miles.

The large number of pollen grains of *D. mawsonii* in residues of most Australian deposits indicates that a conifer, allied to the living species *D. franklinii* was a component of the Early and Middle Tertiary floras of Australia and Tasmania. In many of these deposits podocarps, including probably *Dacrydium*, are present as megascopic fossils.

The occurrence of examples of the sporomorph *D. mawsonii* in Western Australia is of considerable interest, suggesting the pan-Australian Tertiary flora anticipated by Herbert (1950). However, at this stage of our knowledge the presence of such a flora is not proved because:

(1) The number of pollen grains of the *D. mawsonii* type is relatively few, i.e. the possibility of their long-range transport by wind must be taken into account.

(2) There are as yet no records of megascopic plant remains of *Nothofagus* and podocarps so common in Tertiary deposits of eastern Australia.

Thus, while there is a strong suggestion of the presence of the Tertiary temperate rain forest in Western Australia, this cannot be considered proved until there is better evidence than that at present available.

V. Acknowledgments

It is a pleasure to acknowledge indebtedness to Dr. Winifred Curtis, University of Tasmania, and Mr. T. E. Burns of Launceston for male cones of *Dacrydium franklinii*; to Dr. Rhodes Fairbridge, University of Western Australia, for geological samples; to Dr. D. E. Thomas, Mines Department, Melbourne, for the accompanying map; and to Dr. A. B. Edwards, Mineragraphic Investigations, C.S.I.R.O., Melbourne; Mr. E. D. Gill, National Museum, Melbourne; and Mr. J. W. Lillywhite, Meteorological Bureau, Melbourne, for information and advice.

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EXPLANATION OF PLATE 1

All the figures are from untouched negatives; the pollen grains in Figures 1-22 are magnified about 600 times; those in Figures 23-27 about 630 times.

Figs. 1, 2.—*Dacrydium franklinii.* Optical section, proximal view of a fully expanded acetolysed pollen grain from Corinna, Tas.

Figs. 3, 4.—*Dacrydium franklinii.* Lateral views of grains from Corinna, Tas.

Fig. 5.—*Dacrydium franklinii.* Unexpanded, non-acetolysed pollen grain from same locality.

Figs. 6, 7.—*Dacrydium franklinii.* Immature pollen grains from cones collected near Lake Vera, Tas., about 6 months prior to maturity.

Fig. 8.—*Dacrydium franklinii.* Two grains of a tetrad from Lake Vera.

Figs. 9-11.—*Dacrydiumites mawsonii.* Pollen grains from Vegetable Creek, N.S.W.

Fig. 12.—*Dacrydiumites mawsonii.* Distal view of unexpanded pollen grain from S.E.C. bore 263, 200-210 ft. Loy Yang, Vic.

Figs. 13, 14.—*Dacrydiumites mawsonii.* Fully expanded and unexpanded pollen grains from Anglesea, Vic.

Fig. 15.—*Dacrydiumites mawsonii.* Distal view of pollen grain from 32 ft. from top of coal, Yallourn, Vic.

Fig. 16.—*Dacrydiumites mawsonii.* Oblique view of pollen grain from brown coal, Moorlands, S.A.

Fig. 17.—*Dacrydiumites mawsonii.* Distal view of partially expanded grain showing wide furrow, texture of cap, and striations in proximal tubercle. Cootabarlow, S.A.

Fig. 18.—*Dacrydiumites mawsonii.* Distal view of unexpanded grain from bore, 36-42 ft., Pidinga, S.A.

Fig. 19.—*Dacrydiumites mawsonii.* Pollen grain from bore 2009. Trevallyn, Tas.

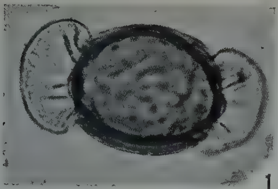
Figs. 20, 21.—*Dacrydiumites mawsonii.* Pollen grain from "coffee rock" specimen 8662/1, Geol. Dept., Univ. W.A.

Fig. 22.—*Dacrydiumites mawsonii.* Pollen grain from specimen 8662/9, Geol. Dept., Univ. W.A.

Figs. 23-26.—*Dacrydiumites mawsonii.* Pollen grains from lignite near Port Jeanne d'Arc, Kerguelen Archipelago.

Fig. 27.—*Dacrydiumites ruei.* Distal view of pollen grain from lignite near Port Jeanne d'Arc, Kerguelen Archipelago.

DACRYDIUMITES IN SOUTHERN TERTIARY DEPOSITS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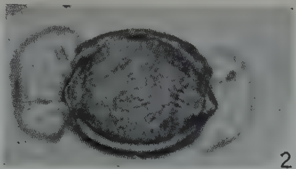
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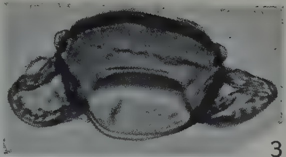
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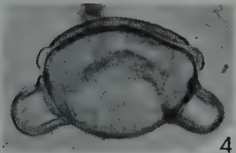
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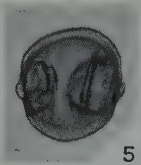
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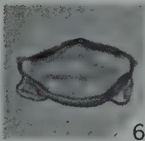
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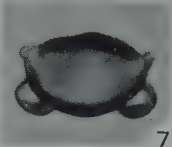
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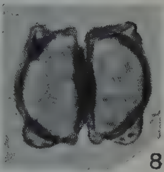
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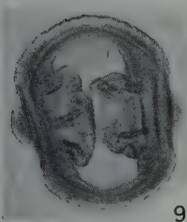
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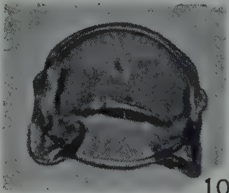
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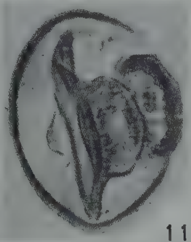
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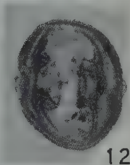
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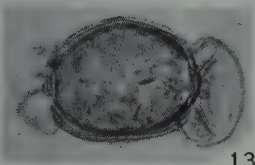
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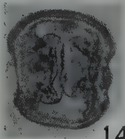
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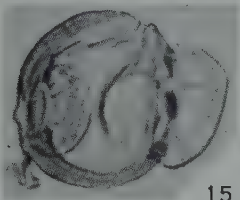
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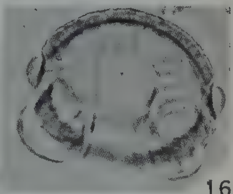
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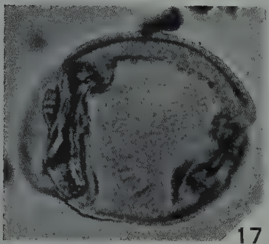
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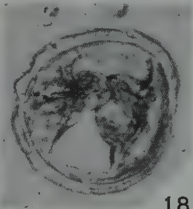
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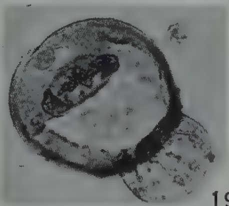
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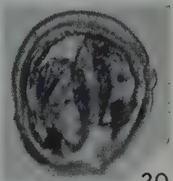
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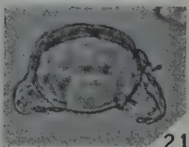
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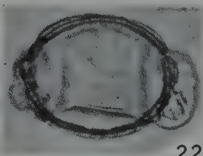
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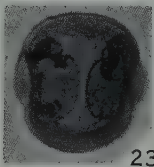
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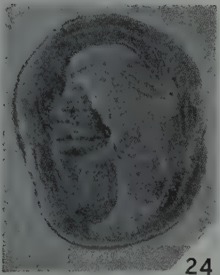
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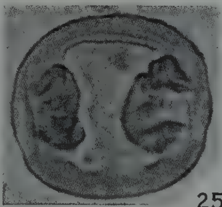
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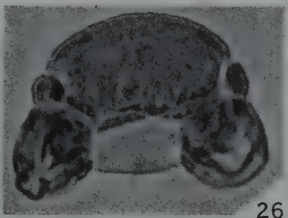
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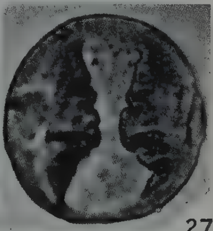
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THE TERTIARY OCCURRENCE AND DISTRIBUTION OF *PODOCARPUS* (SECTION DACRYCARPUS) IN AUSTRALIA AND TASMANIA

By Isabel C. Cookson* and Kathleen M. Pike*

[*Manuscript received August* 27, 1952]

Summary

Proof of the occurrence of the section Dacrycarpus of the genus *Podocarpus* in Australia and Tasmania is presented.

Foliage shoots with structure preserved from Yallourn, Victoria, have been designated hypotypes of *Podocarpus praecupressinus* Ett.

Pollen grains of the Dacrycarpus type have been identified in a number of widely separated Tertiary deposits. The sporotype *Dacrycarpites* has been instituted for them and one sporomorph *Dacrycarpites australiensis* described.

I. Introduction

Although the section Dacrycarpus of the genus *Podocarpus* is not represented at present, in either Australia or Tasmania, several authors have suggested that it occurred there during the Tertiary period (Florin 1940).

The first of these was Ettingshausen, who in 1888 referred certain sterile shoots and a berry-like fruit from Vegetable Creek (Emmaville) in north-eastern New South Wales to this section under the name *Podocarpus praecupressinus*, the specific name having been chosen on account of resemblances to the recent species *P. imbricatus* (syn. *P. cupressinus* R.Br.).

Subsequently Deane (1902) and Paterson (1935) identified specimens from Wingello, in south-eastern New South Wales, and Narracan, in south-eastern Victoria respectively, with *P. praecupressinus* (wrongly written *P. praecupressiformis*). In 1950 Selling recorded small bilateral shoots of the *P. praecupressinus* type from northern Tasmania and southern Queensland under the name "*Podocarpus* sp. (sect. Dacrycarpus)."

While little doubt regarding the taxonomic position of *P. praecupressinus* has been entertained, no actual proof of its connection with the section Dacrycarpus has hitherto been forthcoming. In this paper structural evidence obtained from shoots morphologically similar to those of *P. praecupressinus*, which fully establishes such a connection, will be presented. The distribution of Dacrycarpus, as indicated by the occurrence in various Tertiary deposits of three-winged pollen grains conformable to those of the recent species, will also be dealt with. By this means it will be shown that the section was widely distributed in Australia and Tasmania during the early Tertiary period and that it persisted, in some areas at least, until the Upper Pliocene.

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* Botany Department, University of Melbourne.

II. Fossil Shoots of Podocarpus praecupressinus Ett. from Victoria

(*a*) *General Considerations*

Shoots similar to those of *P. praecupressinus* have been found at various levels in the brown coal at Yallourn, Vic., but most abundantly in a bed exposed on the west face of the third level in 1950, the coordinates of which were 300W., 7000S., and reduced level 62. A few examples were also obtained from a sandy layer on top of the coal at the Lucifer Mine, Bacchus Marsh, Vic., but these have not added any further information to that provided by the more complete specimens from Yallourn.

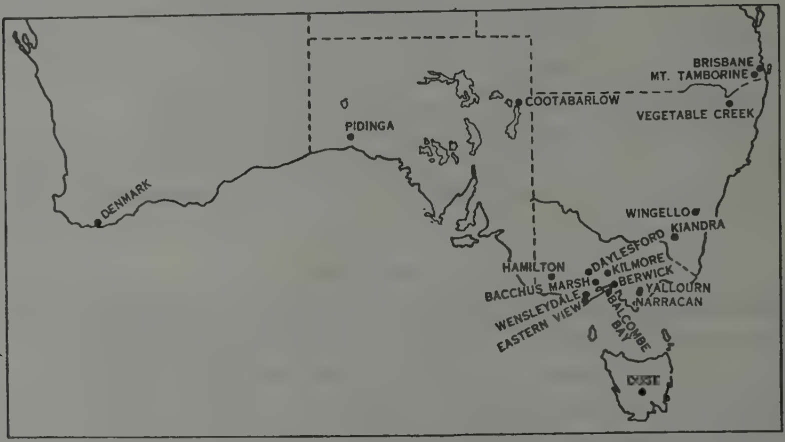

Fig. 1.—Map of southern Australia with localities mentioned.

Both the small distichous axes with spreading bilateral leaves and radiosymmetrical twigs with scale-like bifacial leaves that constitute *P. praecupressinus* occur at Yallourn. They were found in considerable numbers in the particular bed referred to above, but no organic connection between the two types has been observed. The normal occurrence, however, of dimorphic shoots of similar form in living species of *Podocarpus* (section Dacrycarpus) supports the view expressed earlier by Ettingshausen (1888), Florin (1940), and others that shoots of the *P. praecupressinus* type are detached portions of the dimorphic branch systems of this section. This conclusion has been verified during the present investigation by the discovery of a close agreement between the leaf cuticles of the Yallourn specimens and those of living species such as *P. imbricatus* Blume, *P. dacrydioides* A. Rich., *P. papuanus* Ridl., and *P. vieillardii* Parl.

Considerable morphological and anatomical uniformity exists within the section Dacrycarpus. Small differences in both respects occur between the species (Florin 1931) but these are so slight and variable that the identification of disconnected sterile twigs is neither easy nor reliable. This being so, the separation of fossil species within one geographical area on purely vegetative characters seems likely to be even more difficult and uncertain. It is therefore proposed to use Ettingshausen's name *Podocarpus praecupressinus*, originally applied to a "form" species (known only from fragmentary impressions) for a Victorian species in which details of leaf structure are known.

Specimens from Yallourn are hereby designated hypotypes of *Podocarpus praecupressinus* Ett., since this narrows the application of the name and provides characters by which the species may be more accurately defined.

(*b*) *External Characters of* P. praecupressinus *from Yallourn, Vic.*

(i) *Sterile Branches with Dimorphic Leaves* (Plate 1, Figs. 1-5).—Each branchlet consists of a slender axis on which both bilateral and bifacial leaves are closely and spirally inserted. The majority of leaves are bilateral and 2-ranked; they are linear, entire, straight or somewhat falcate, 2.5 mm. long and 0.5-1 mm. broad, decurrent at the base, the largest occupying the middle of the shoot; the apex is mucronate, the mucro usually being sharply incurved; there is a single prominent midrib, and the margin is entire. At the base of the shoot the leaves are small bifacial scales, linear-triangular, broadly keeled, and radially arranged.

(ii) *Axes with Bifacial Leaves Only* (Plate 1, Figs. 9-13).—The specimens of this type are short lengths of slender, unbranched axes 1-2 mm. in diameter; in a few (Plate 1, Figs. 9, 10) the terminal buds are preserved. Occasionally detached buds (Plate 1, Fig. 16) very similar to young male shoots of living species have been observed. Twigs of this type bear small, awl-shaped, spirally arranged, uninerved, bifacial leaves of variable size. The leaves are linear-lanceolate, sometimes slightly falcate and keeled, often closely appressed to the stem, with an acute or acuminate apex that is either straight or directed towards the axis, and a broadly decurrent, tapering base.

(*c*) *Cuticular Structure of Leaves of* P. praecupressinus *from Yallourn*

(i) *Bilateral Leaves* (Plate 1, Fig. 17; Plate 2, Figs. 20, 24).—Amphistomatic with the stomata restricted to 2 longitudinal bands extending from apex to base on each surface. These bands consist of from 1 to 6 longitudinal rows of stomata, the bands adjacent to the upper edge of the leaf being wider than those near the lower edge. The stomata are oriented parallel to the long axis of the leaf. Each is surrounded by a ring of 4-6 subsidiary cells, most commonly 4, 2 of which are always polar; sometimes each stomatal group includes a complete set of encircling cells but usually the polar ones are absent. Frequently 2 stomatal groups have a polar subsidiary cell in common. The cuticle of the subsidiary cells is somewhat thicker than that of the neighbouring epidermal cells.

The epidermal cells which are arranged in longitudinal rows have thin, straight, weakly pitted lateral walls. The cells at the edge of the leaf are unmodified.

(ii) *Bifacial Leaves* (Plate 1, Figs. 18, 19; Plate 2, Figs. 21, 22, 23).—Amphistomatic; the stomata are confined to 2 more or less continuous bands on each surface, those of the lower surface being narrower and sometimes shorter than those of the upper surface. The stomatal bands are separated from one another by stomata-free parenchyma. The number of stomata is considerably reduced in the small bifacial scales at the bases of the sterile bilateral shoots. The stomatal groups are similar in all respects to those of the bilateral leaves.

The epidermal cells are longitudinally oriented; their lateral walls are straight, moderately thin, and rather strongly pitted. The edges of the leaves are entire and partially or completely composed of ctenoidally arranged cells, which in surface view under a relatively low magnification give the margin a "frill"-like appearance. In the bifacial leaves of larger twigs the "frill" is restricted to the apical region (Plate 1, Fig. 18). In the small scales of the sterile bilateral shoots it frequently extends almost to the base (Plate 1, Fig. 19).

(*d*) *Internal Anatomy* (Plate 2, Figs. 25, 26)

The tissues of the Yallourn specimens of *Podocarpus praecupressinus* are considerably compressed and the mesophyll of the leaves is badly preserved. However, some of the structural features of both bifacial and bilateral leaves have been seen in the sections cut by the paraffin method.

The epidermal cells are small, square to quadrangular in cross section, and their outer walls are about 3 μ thick. Beneath the epidermis on both surfaces is a single layer of thick-walled hypodermal fibres broken only at the stomata, which occur at intervals on both surfaces. The guard cells lie obliquely to and slightly beneath the level of the epidermis. They have thick outer and inner walls and are overarched by projections from the subsidiary cells. The encircling cells are indistinguishable from ordinary epidermal cells.

A single large resin canal occurs in the centre of the bifacial leaves beneath the vascular bundle, the xylem of which can sometimes be distinguished. Resin canals have not been detected in the bilateral leaves but this is probably due to faulty preservation.

III. Comparisons of Podocarpus praecupressinus with Recent and Fossil Species

(*a*) *Recent Species*

Although Ettingshausen (1888) noted a likeness between shoots of *P. praecupressinus* and *P. imbricatus,* the uniformity in external features within the section Dacrycarpus makes it difficult to single out any one species as being most like *P. praecupressinus.* The sterile branches with dimorphic leaves from Yallourn seem to be smaller than those of recent species.

The uniformity of the epidermis within the section Dacrycarpus has been remarked upon more than once by Florin (1931, 1940) so that it is not surprising that the epidermal features of *P. praecupressinus,* although clearly those of the section, do not suggest a trend towards any particular living species.

The internal structure confirms the identity of *P. praecupressinus* with Dacrycarpus. As in the living species there is a hypodermis on both surfaces broken only by the stomata and in the bifacial leaves a single resin canal beneath the mid vein (Buchholz and Gray 1948). The stomata agree exactly with those of recent species (Florin 1931, Fig. 74*c*).

(*b*) *Fossil Species*

A few extra-Australian Tertiary species of the section Dacrycarpus have been described. The most completely known of these is *Podocarpus inopinatus* Florin (1940) from Eocene beds in south Chile. The descriptions of the sterile shoots with dimorphic leaves and the epidermis of the bilateral leaves agree closely with those given for *Podocarpus praecupressinus* and there is no doubt that the two species were closely related.

Representatives of Dacrycarpus have been described from Eocene beds of the South Island of New Zealand (Florin 1940) but, as yet, these are imperfectly known and cannot be satisfactorily compared with *Podocarpus praecupressinus.*

IV. Pollen Grains of Recent and Tertiary Species of Podocarpus (Section Dacrycarpus)

(*a*) *Recent Species*

(i) *General Considerations*

The 3-winged character of the pollen grains of *Podocarpus dacrydioides* has long been known (Thibout 1896; Stiles 1912; Sinnott 1913). This feature has also been recorded for pollen of *P. imbricatus* by Florin (1931, p. 285) who at the same time suggested that it might be characteristic of Dacrycarpus as a whole. This idea was again put forward by Wodehouse (1935) but no attempt to check it seems to have been made either then or subsequently.

During the present investigation more information in this connection was needed for the identification of the larger 3-winged pollen grains that occur in pollen residues derived from Australian Tertiary deposits. An examination of the pollen of *P. dacrydioides, P. imbricatus, P. papuanus,* and *P. vieillardii* was undertaken, the results of which show that the pollen grains of all these species have 3 bladders and that only minor differences, sometimes difficult to detect, occur between them. Since a pollen diagnosis of only one of these types — *P. dacrydioides* — has been published, descriptions of the pollen of the other 3 species are included in this paper. For convenience and completeness the exhaustive description of the pollen of *P. dacrydioides* given by Cranwell (1940) is quoted in full.

(ii) *Pollen Descriptions*

(1) *Podocarpus dacrydioides* (Plate 3, Figs. 40-42).—"Grain large, sphaeroidal or rather lens-shaped, the proximal side more rounded than the distal, ranging from 42 to 52 μ across and 33 to 43 μ deep, or equal to the diameter, but mainly very uniform, about 46 μ across. Furrow wide, about 25 μ, triangular to roughly circular, bounded by 3 comparatively large, pale, weak bladders, which are rounded in outline, about 30 μ deep by 45 μ long, very often fused or overlapping. Furrow rims not very distinct. When expanded, the bladders fold in, revealing only a narrow triradiate area of the furrow membrane. Exine 2-walled, about 3.2 μ on middle of dorsal cap, texture coarsely granular to reticulate, strengthening to form a strongly wrinkled marginal ridge, then merging

gradually into the bladders, which have a smooth, thin wall with delicate, often confused, internal thickenings laid down as fine meshes 3-4 μ apart; more crowded near the ventral roots. Size overall about 75 μ."

(2) *Podocarpus imbricatus* (Plate 3, Figs. 32-35).—Grain large. Body spherical, circular to triangular in polar view, 32-50 μ in diameter. Wings 3, large, either meeting laterally or with a space between, 15-24 μ deep, 38-47 μ wide, with a wide-meshed reticulum; overall diameter of grain including bladders from 50 to 70 μ. Furrow fairly wide. Exine 2-layered. Sculpture over the cap apparently rugulate (Faegri and Iversen 1950, p. 21), fine over the proximal pole, becoming coarse towards the points of insertion of the wings.

Source of material.—Botanical Gardens, Tjibodas coll. C. A. Sargent ex Herbarium, Missouri Botanical Garden; Mountain Garden, Tjibodas, plot E, tree no. 13, 1952.

The pollen of *P. imbricatus* seems to be the most variable of the Dacrycarpus types examined. Whilst typically the grains are large, approaching if not equalling those of *P. dacrydioides* in overall diameters, many small examples have occurred in all the preparations whether derived from single cones or several of the same collection. Some of the small grains have imperfectly developed wings, very thick marginal rims, and a coarser sculpturing of the cap than is usual. These aberrant grains have not been included in the description just given.

(3) *P. papuanus* (Plate 3, Figs. 36-39).—Grain medium with a relatively small body, 27-36 μ in diameter and 23-32 μ deep, and 3 large, deep wings 32-40 μ long and 21-33 μ deep, which usually meet one another laterally; reticulum wide-meshed in large grains, indistinct in small ones. The overall length of the grain including the bladders ranges from 47 to 65 μ. Furrow fairly wide. Exine 2-layered, 2.6 μ in dorsal region of cap; its sculpture in this region appears to be finely rugulate, becoming more coarsely so towards the points of insertion of the bladders. Marginal rim dense and prominent, 3-5 μ thick, margin finely crenate.

Source of material.—Western New Guinea, L. T. Brass No. 13084; Dutch New Guinea. A. F. Wollaston Expedition 1912-13 (Type) ex. British Museum.

(4) *P. vieillardii* (Plate 3, Figs. 43-45).—Grain comparatively small; body 27-36 μ in diameter and 23-29 μ deep. Bladders 3, small, shallow, 23-34 μ long and 13-18 μ deep, usually not meeting laterally, meshes of reticulum frequently ill defined. Overall diameters of grains 38-47 μ. Furrow wide. Exine 2-layered, the sculpture of the cap, which appears to be of the rugulate type, having a coarser texture than that of *P. dacrydioides, P. imbricatus,* and *P. papuanus.* Marginal rim distinct, 3-6 μ wide, outer edge coarsely crenate.

Source of material.—New Caledonia, Buchholz collection No. 1140.

(iii) *Comparisons*

The pollen grains of *P. dacrydioides* and *P. imbricatus* in their typical forms are very similar to one another and both are considerably larger than those of *P. papuanus* and *P. vieillardii.* However, the wide size range, which on the evidence of several distinct collections seems to be a usual feature of the pollen of *P. imbricatus*, decreases the usefulness of overall and body diameters as a distinguishing feature.

The large proportion of small, thicker-walled grains in some of the preparations of *P. imbricatus* has already been referred to. These aberrant grains approach those of *P. papuanus* and *P. vieillardii* in size and the latter in the coarseness of the texture of the cap. The occurrence of such a variation considerably increases the difficulty that would normally be experienced in the separation of individual grains in a pollen mixture of all four types.

Before leaving this subject attention should be drawn to the rather close resemblance between the pollen grains of *P. vieillardii* and those of *Microcachrys tetragona* (Erdtman 1943). Both types have bodies of similar diameters, small bladders that do not meet, and prominent marginal rims. The pollen grains of *Microcachrys* differ from those of *P. vieillardii* in having more widely spaced bladders, a wider furrow, and finer sculpture of the cap.

(*b*) *Fossil Species*

Dacrycarpites n. spt.

This sporotype is proposed for isolated medium to large 3-winged fossil pollen grains with a similar construction to those of living species of *Podocarpus* (section Dacrycarpus).

Grains of this type have been observed in many Australian and Tasmanian ligneous deposits. Usually their frequencies have been low but occasionally, as in the deposits at Vegetable Creek, Yallourn, and Hamilton, they have been relatively numerous. As yet, it has not been possible to directly connect any of them with megascopic remains of the *Podocarpus praecupressinus* type with which in several instances they have been associated.

At first it was thought that at least two sporomorphs of *Dacrycarpus* could be recognized, one typified by large grains comparable to those of *P. dacrydioides* and *P. imbricatus* with bodies 40 μ or more in diameter, and another by small grains nearer to those of *P. papuanus* and *P. vieillardii* with bodies about 35 μ or less in diameter. The distinction between the large and small types appeared to be further increased by the coarser sculpture of the cap evident in the smaller grains, a feature in which they seemed to approach the pollen of *P. vieillardii* rather than that of *P. papuanus*.

It was only after a careful study of the pollen of *P. imbricatus* had shown that a large proportion of small pollen grains can occur in pollen samples of this species that the doubtful value of size as a basis for the separation of sporomorphs of *Dacrycarpites* was realized. Moreover, the occurrence of a coarser type of sculpture in the proximal region of the cap of some of the smaller grains of *P. imbricatus* (Section IV (*a*) (ii)) similar to that of *P. vieillardii* on the one hand and some of the small grains of *Dacrycarpites* on the other, further emphasized how doubtful sporomorph identifications would be if determined on either or both of these bases.

In view of these facts it was finally decided to include all isolated pollen grains of the Dacrycarpus type, irrespective of size, age, or locality in one generalized sporomorph *Dacrycarpites australiensis*.

Dacrycarpites australiensis n. spm.

Plate 2, Figs. 27-31; Plate 3, Figs. 46-51

Grain medium to large; body circular or triangular in polar view, 30-63 μ in diameter (Table 1); bladders 3, 36-56 μ long and 16-32 μ deep, either with a space between them or meeting laterally, usually inserted along the sides of the body, reticulum well defined in large examples, often obscure in the smaller ones. Furrow wide, usually triangular. Exine 2-layered, sculpture finely rugulate, becoming coarsely so towards the insertion of the bladders in the larger grains, more coarsely and uniformly rugulate in some of the small grains, with the vallae (Faegri and Iversen 1950) polygonal in shape. Marginal rim 2.5-7 μ thick, the outer edge finely to coarsely crenate.

TABLE 1

BODY DIAMETERS OF *DACRYCARPITES AUSTRALIENSIS* FROM AUSTRALIAN DEPOSITS

Location	Range in Diameter of Body (μ)
Queensland	
Mt. Tamborine ..	30-45
New South Wales	
Vegetable Creek ..	43-63
Victoria	
Yallourn	32-52
Berwick	34-52
Balcombe Bay ..	34-52
Kilmore	31-48
Hamilton	31-50
South Australia	
Cootabarlow ..	34-45
Pidinga	34-63
Western Australia	
Denmark	31
Tasmania	
Ouse	36-56

Distribution.—The asterisk indicates deposits in which megascopic remains of *P. praecupressinus* have occurred.

Queensland: Mount Tamborine. Carbonaceous clay under basalt about 300 yd. below Curtis' Falls, Cedar Creek, collector E. D. Gill. Age: Pliocene according to Bryan and Jones (1946).

New South Wales: *Vegetable Creek (Emmaville). Mudstone from deep leads. Melb. Univ. Geol. Dept. No. 242. Age: ? Oligocene.

Kiandra. New Chum Hill. Soft ligneous shale 135 ft. below the basalt. Portion of Dr. Dulhunty's coal sample 103. Nat. Mus. Vic. No. P.15710.

Victoria: Yallourn. Pollen coal (Edwards 1947, p. 27). Ligneous clay from fruit zone near floor of Open Cut. *Brown coal at various horizons in the Open Cut. Age: Oligocene.

Loy Yang: Brown coal throughout bore 263. Age: Oligocene.

Berwick: Sub-basaltic clay underlying Older Basalt at Wilson's Quarry. Age: Oligocene. Nat. Mus. Vic. No. P.15680.

*Bacchus Marsh. Coal from Lucifer mine. Age: ? Oligocene. Mus. Vic. No. P.15724.

Bacchus Marsh. Coal from Lucifer mine. Age: ? Oligocene.

Anglesea. Black carbonaceous sandstone from coastal cliff near mouth of Anglesea River. Age: ? Middle Eocene, according to Raggatt and Crespin (1952).

Eastern View, near Anglesea. Upper of two carbonaceous beds outcropping on beach opposite to Sprouts' Creek. Age: Raggatt and Crespin (1952) are of the opinion that these beds are Palaeocene to Lower Eocene.

Wensleydale. Clay parting in coal. Age: Oligocene. G.S.V. 50083.

Balcombe Bay. Mudstone containing leaf remains from coastal cliff. Age: Miocene.

Hamilton. Carbonaceous clay on north side of Grange Burn. Age: Upper Pliocene.

Stony Creek, Daylesford. Ligneous clay. Age: Middle Pliocene (Coulson 1950).

South Australia: Pidinga. Lignite from S.A. Dept. of Mines bore P.15, 35 miles south-east of Ooldea. Age: Tertiary.

Cootabarlow. Carbonaceous shale. S.A. Dept. of Mines bore at 493-515 and 573 ft. Age: ? Early Tertiary.

Western Australia: Hay-Denmark Railway, deviation at 354 miles. Carbonaceous sandy deposit 50 ft. below surface, "coffee rock." Age: Tertiary. Geol. Dept. Univ. W.A. No. 8662-1.

Tasmania: Ouse. Lignitic seam in the Ouse River, about 400 yd. upstream from Bridge Hotel. Age: ? Oligocene.

V. TERTIARY DISTRIBUTION OF PODOCARPUS (SECTION DACRYCARPUS) IN AUSTRALIA AND TASMANIA

The occurrence of shoots of *Podocarpus praecupressinus* in southern Queensland (Selling 1950); New South Wales (Ettingshausen 1888; Deane 1902); Victoria (Paterson 1935; and this paper); and Tasmania (Selling 1950; and this paper) indicates the wide distribution this type must have had in the eastern portion of Tertiary Australia. However, the presence of the sporomorph *Dacrycarpites australiensis* in deposits in which *Podocarpus praecupressinus* does not occur has shown that the section Dacrycarpus was not restricted only to this eastern area. It has now been traced in a westerly direction to Cootabarlow and Pidinga in South Australia and to the Denmark area in Western Australia.

Since very little is known at present of the Tertiary flora of Western Australia, it is of interest to find the sporomorphs *Dacrycarpites australiensis* and

Dacrydiumites mawsonii associated together there. However, the small number of examples of the former encountered raises the question discussed previously in connection with the western occurrence of *D. mawsonii* (Cookson 1953, Section IV) as to whether they might not have been transported from more easterly localities.

Nothing can be reported regarding the occurrence of the section Dacrycarpus in northern Australia, or New Guinea where it now has three living representatives. Several Cretaceous, Miocene, and Pliocene coaly deposits from New Guinea have been examined but so far no examples of the sporomorph *Dacrycarpites australiensis* have been seen.

The ages of most of the Tertiary deposits mentioned in this paper are not yet indisputably determined. It is therefore not possible to indicate the exact period during which the section Dacrycarpus retreated northwards. Florin (1940, p. 88) states that "It probably disappeared from South America, Antarctica, and eastern Australia in the Neogene."

The occurrence of the sporomorph *Dacrycarpites australiensis* in a carbonaceous deposits at Hamilton, the age of which is estimated by Gill (1952) on the evidence of associated shelly fossils to be probably Upper Pliocene, is therefore of importance. If this estimation is correct it would seem that the section Dacrycarpus of *Podocarpus* was still in existence in Victoria during late Pliocene times.

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Explanation of Plates 1-3

All the photographs are from untouched negatives

Plate 1

Fig. 1.—*Podocarpus praecupressinus.* Shoots with bilateral leaves from Yallourn, Vic. Natural size. Nat. Mus. Vic. No. P. 15713.

Fig. 2.—*Podocarpus praecupressinus.* Shoot with dimorphic leaves from Yallourn. Natural size. Nat. Mus. Vic. No. P. 15714.

Fig. 3.—*Podocarpus praecupressinus.* The same shoot × 3.

Fig. 4.—*Podocarpus praecupressinus.* Another sterile shoot with dimorphic leaves from Yallourn. Natural size. Nat. Mus. Vic. No. P. 15715.

Fig. 5.—*Podocarpus praecupressinus.* The same shoot × 2.

Figs. 6, 7.—*Podocarpus praecupressinus.* Portions of shoots with bilateral leaves from Bacchus Marsh. × 3. Nat. Mus. Vic. Nos. P. 15723, 15716 respectively.

Fig. 8.—*Podocarpus vieillardii.* A shoot with dimorphic leaves from New Caledonia. Natural size. Buchholz Collection No. 1140.

Figs. 9, 10.—*Podocarpus praecupressinus.* Two shoots with bifacial leaves from Yallourn showing terminal buds × 6. Fig. 10. Nat. Mus. Vic. No. P. 15717.

Fig. 11.—*Podocarpus praecupressinus.* A fragment of a shoot with bifacial leaves showing a small lateral bud. × 4. Nat. Mus. Vic. No. P. 15713.

Fig. 12.—*Podocarpus praecupressinus.* A twig with bifacial leaves from Yallourn. × 3. Nat. Mus. Vic. No. P. 15720.

Fig. 13.—*Podocarpus praecupressinus.* Another twig with bifacial leaves from Yallourn. ×5. Nat. Mus. Vic. No. 15721.

Fig. 14.—*Podocarpus praecupressinus.* A small branchlet with bifacial leaves which become smaller and more broadly triangular distally. × 5.

Fig. 15.—*Podocarpus papuanus.*—A young male shoot. × 4.

Fig. 16.—*Podocarpus praecupressinus.* A possible young male shoot from Yallourn. × 5. Nat. Mus. Vic. No. P. 15722.

Fig. 17.—*Podocarpus praecupressinus.* Cuticle of apical region of a bilateral leaf. × 90. Nat. Mus. Vic. No. P. 15738.

Fig. 18.—*Podocarpus praecupressinus.* Cuticle of bifacial leaf showing the acuminate apex and marginal frill. × 90. Nat. Mus. Vic. No. P. 15739.

Fig. 19.—*Podocarpus praecupressinus.* Cuticle of bifacial scale from base of a dimorphic shoot. × 90. Nat. Mus. Vic. No. P. 15740.

Plate 2

Fig. 20.—*Podocarpus praecupressinus.* Cuticle of a bilateral leaf opened out to show stomatal bands. × 35. Nat. Mus. Vic. No. P. 15741.

Figs. 21, 22.—*Podocarpus praecupressinus.* Cuticles of two bifacial leaves opened out to show stomatal bands. × 35. Nat. Mus. Vic. Nos. P. 15742-3 respectively.

Fig. 23.—*Podocarpus praecupressinus.* Cuticle from margin of a bifacial leaf showing ctenoidally arranged cells. × 300. Nat. Mus. Vic. No. P. 15744.

Fig. 24.—*Podocarpus praecupressinus.* Three stomatal groups with four and six subsidiary cells. × 600.

Fig. 25.—*Podocarpus praecupressinus.* Transverse section through a stomatal group, showing two thick-walled guard cells, subsidiary cells, and encircling cells. × 600. Nat. Mus. Vic. No. P. 15745.

Fig. 26.—*Podocarpus praecupressinus.* Transverse section of a bifacial leaf showing epidermis, hypodermis, xylem, and large resin canal. × 150. Nat. Mus. Vic. No. P. 15746.

Fig. 27.—*Dacrycarpites australiensis.* A small pollen grain from Ouse, Tas. × 600.

Figs. 28, 29.—*Dacrycarpites australiensis.* Small grains from Yallourn, Vic. × 600.

Fig. 30.—*Dacrycarpites australiensis.* A small grain from Denmark, W.A. × 600.

Fig. 31.—*Dacrycarpites australiensis.* A small grain from Hamilton, Vic. × 600.

Plate 3

All the figures are of acetolysed pollen grains, magnified 600 times

Figs. 32-34.—*Podocarpus imbricatus.* Three views of a single pollen grain.

Fig. 35.—*Podocarpus imbricatus.* A small pollen grain.

Figs. 36-38.—*Podocarpus papuanus.* Three views of the same pollen grain.

Fig. 39.—*Podocarpus papuanus.* A small example.

Figs. 40-42.—*Podocarpus dacrydioides.* Three views of a single pollen grain.

Figs. 43, 44.—*Podocarpus vieillardii.* Two views of the same pollen grain.

Fig. 45.—*Podocarpus vieillardii.* Proximal region of a pollen grain to show sculpturing of exine.

Fig. 46.—*Dacrycarpites australiensis.* A grain from Hamilton, Vic.

Fig. 47.—*Dacrycarpites australiensis.* A small grain from Pidinga, S.A.

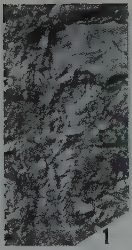
Fig. 48.—*Dacrycarpites australiensis.* A large grain from Pidinga, S.A.

Fig. 49.—*Dacrycarpites australiensis.* An exceptionally large grain from Vegetable Creek, N.S.W.

Fig. 50.—*Dacrycarpites australiensis.* A medium-sized grain from Yallourn, Vic.

Fig. 51.—*Dacrycarpites australiensis.* A large grain from Ouse, Tas.

TERTIARY *PODOCARPUS* IN AUSTRALIA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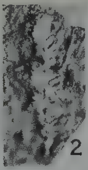
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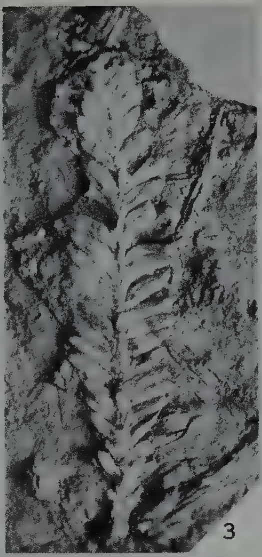
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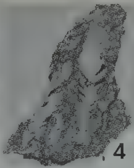
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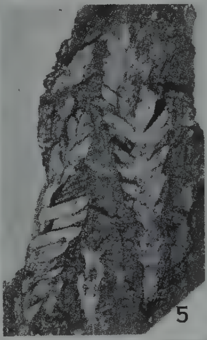
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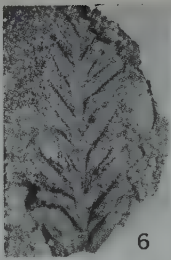
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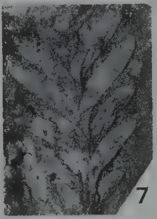
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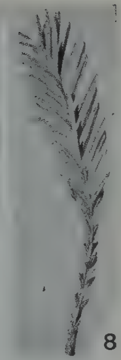
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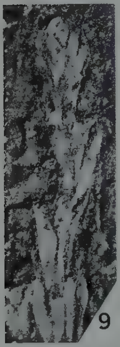
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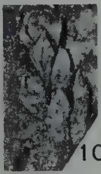
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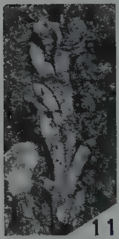
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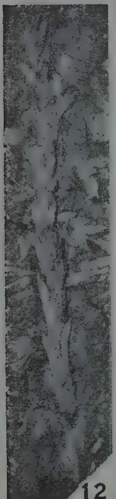
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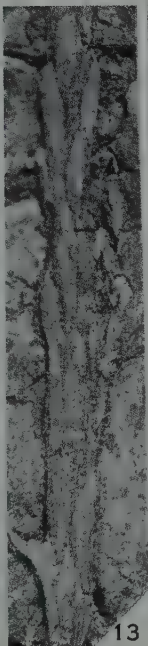
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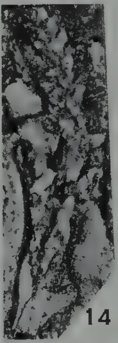
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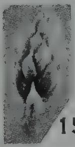
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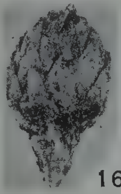
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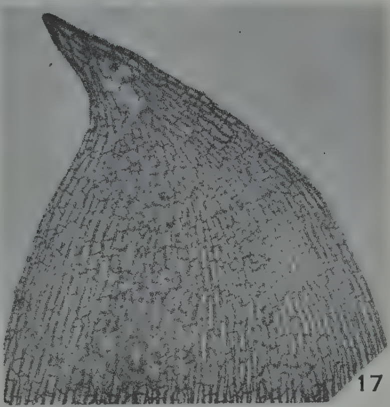
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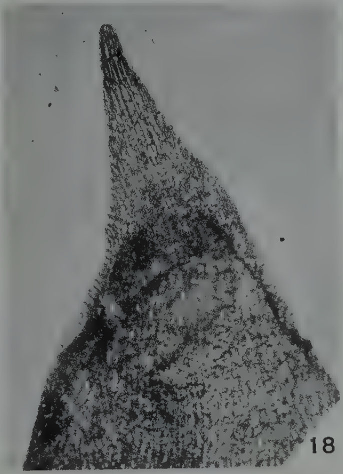
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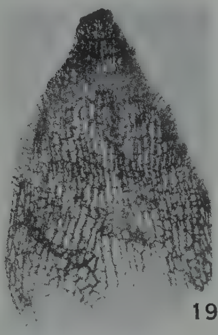
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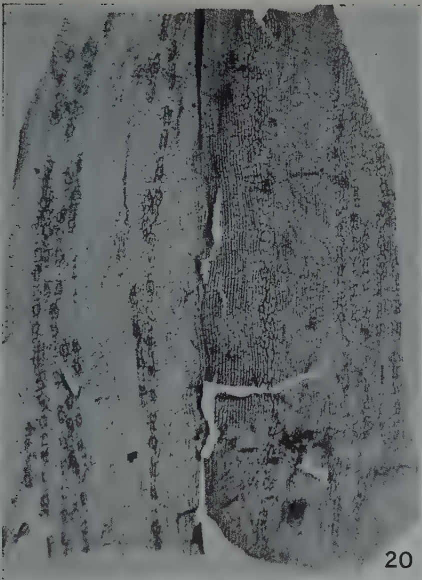
TERTIARY *PODOCARPUS* IN AUSTRALIA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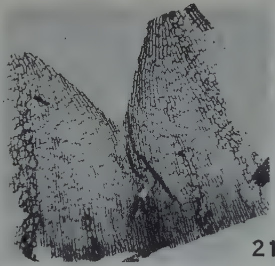
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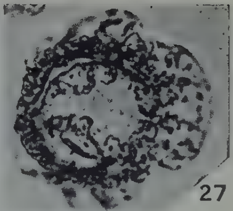
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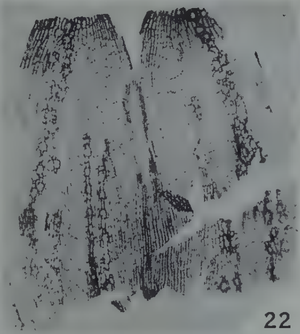
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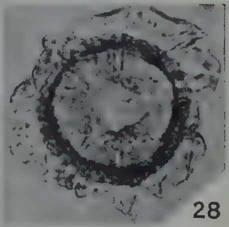
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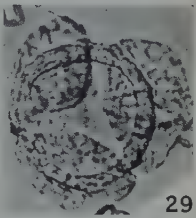
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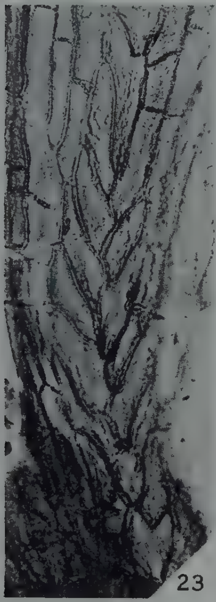
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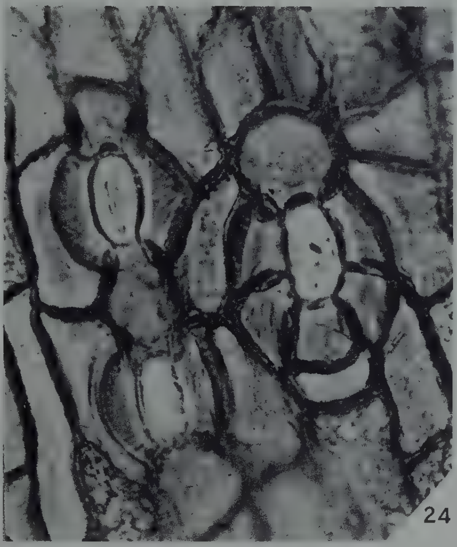
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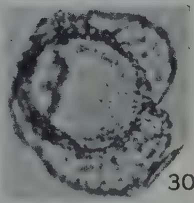
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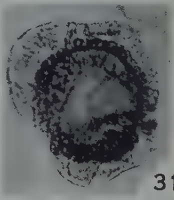
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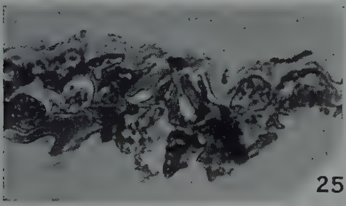
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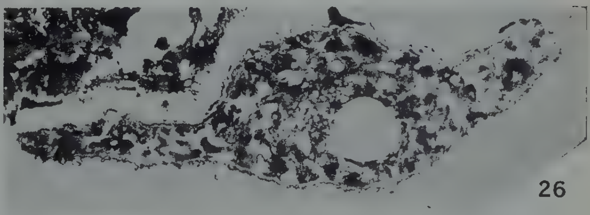
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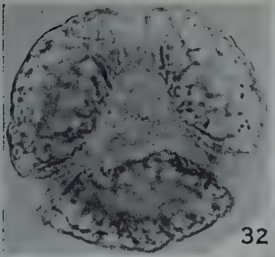
TERTIARY *PODOCARPUS* IN AUSTRALIA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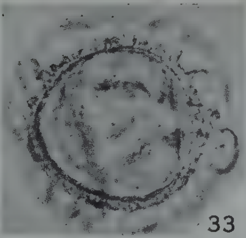
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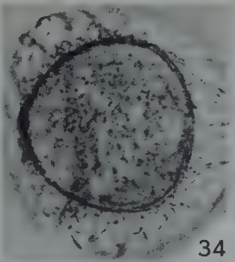
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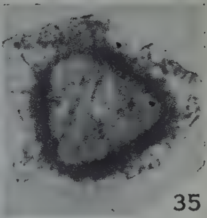
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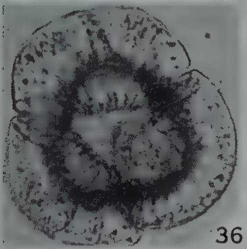
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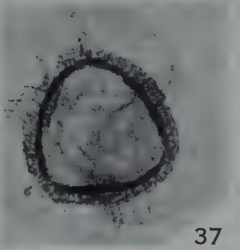
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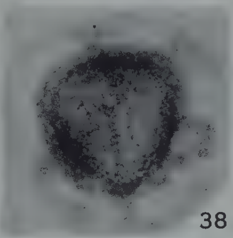
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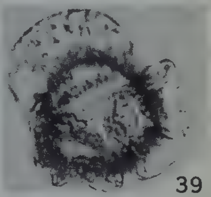
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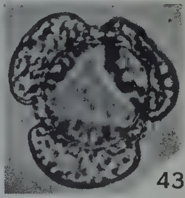
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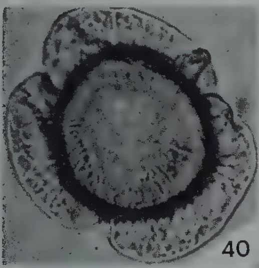
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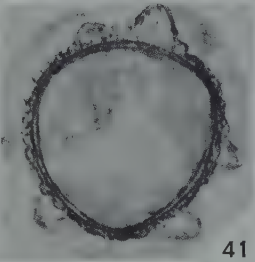
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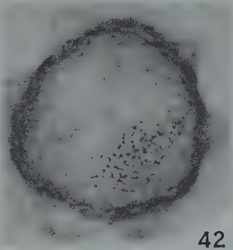
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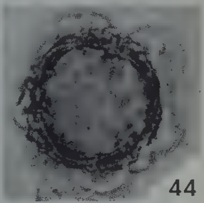
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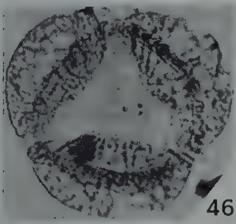
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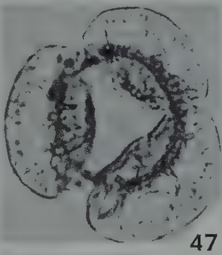
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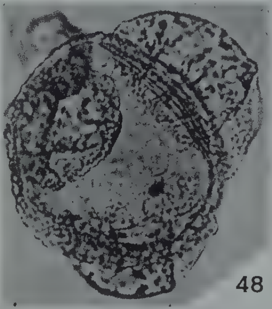
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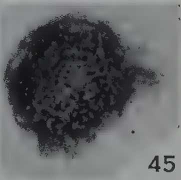
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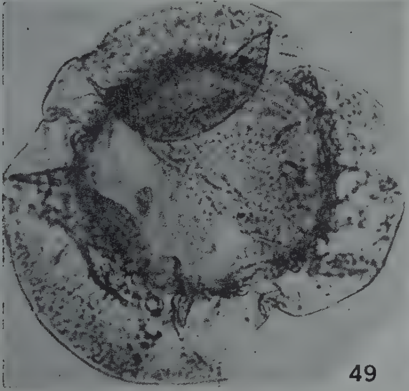
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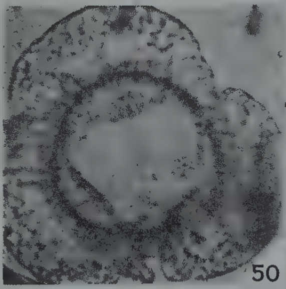
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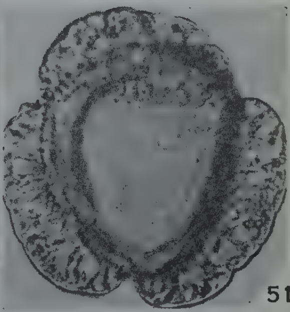
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THE RATE OF PODZOL DEVELOPMENT IN SANDS OF THE WOY WOY DISTRICT, N.S.W.

By A. Burges* and D. P. Drover†

[*Manuscript received July* 3, 1952]

Summary

Soil profiles examined in the parallel sand ridges between Ocean Beach and Woy Woy, N.S.W., show a progressive increase in podzolization as one goes from the beach towards Woy Woy. There is reason to believe that the oldest ridges are about 4000 years old and it is thus possible to suggest a time scale for the leaching of calcium carbonate and the formation of a podzol.

I. Introduction

Most investigators of soil development or plant succession are handicapped by their inability to obtain a time scale for the processes being examined. Only in a few favourable locations in Europe and elsewhere has historical or archaeological evidence enabled the investigators to obtain precise information regarding the rate of soil profile development or plant succession. Salisbury (1925), for instance, was able to estimate the age of various sand dunes by comparison of past and present maps of the Southport district and thus calculate the rate at which calcium carbonate was leached from the dunes. Tamm (1920) studied the rate of podzolization of the soil exposed after the drainage of Lake Ragunda in Sweden. Such favourable opportunities are unfortunately rare. In Australia, no comparable evidence is available; consequently, most attempts to estimate the rate of soil profile development or of plant succession have met with little success.

The area of sand ridges lying to the south of Woy Woy, N.S.W., is one region in which it seems possible to overcome the difficulties imposed by the lack of historical or archaeological evidence. Between Woy Woy Creek and Ocean Beach is an area of country traversed by numerous sand ridges that run parallel to Ocean Beach (Plate 1). The ridges vary in height from 3 to 10 ft. above the general level, the average height of the country above mean sea-level being about 15 ft. While the origin of the parallel ridges cannot be given with certainty, it seems probable that they represent progressive beach fronts formed by the accumulation of sand on the forerunners of Ocean Beach. Colonization of these sand ridges must have taken place soon after they were formed as there is very little evidence of subsequent blowouts or major redistribution of the sand.

Andrews (1912) suggested that the ridges were formed below a water surface and had subsequently been exposed as the result of a recent emergence.

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* Botany School, University of Sydney; present address: The Hartley Botanical Laboratories, University of Liverpool.

† Botany School, University of Sydney; now of the University of Western Australia.

This, however, is most unlikely and the clear-cut evidence of plant succession and varied degree of soil profile development indicates that the ridges nearest to Ocean Beach are the most recent and that as one goes towards Woy Woy the ridges become progressively older.

It now seems generally agreed that there was a eustatic change in sea-level during very recent times and that this led to the exposure of the rock platforms that form such a prominent feature of the central coast of New South Wales. An examination of the topography of the Woy Woy district suggests that such a change in sea-level may well have initiated the deposition of the original sand bar that cut off Woy Woy Creek, and also the formation of the successive beach fronts culminating in Ocean Beach. If this is so then any estimate of the date of the change in sea-level may be used to estimate the age of the sand ridges and hence of their associated soil profiles and plant communities.

Cotton (1926), as the result of his investigation into the rate of sedimentation in the drowned coastal valleys, concluded that this change in level occurred between 3000 and 5000 years ago. Most recent writers (e.g. Browne 1945) have accepted Cotton's estimate and there seems to be a tendency to take the mean figure of 4000 years as fairly correct. If we may assume that this eustatic change in sea-level initiated the parallel ridge formation then a line joining Woy Woy Creek and Ocean Beach may be divided and regarded as a time scale of 4000 years. By this means the age of the soils or plant communities along the line may be readily estimated. Although it is most improbable that the beach building proceeded uniformly throughout the whole period, nevertheless in assuming uniform building the errors introduced will not be large and the estimates of age will still be of the right order of magnitude.

II. Origin and Nature of the Sand

The sand forming the ridges has come from the erosion of the neighbouring sandstone rocks. These are primarily from the Hawkesbury series but sandstones and shales of the Narrabeen series outcrop at sea-level. In the region in which the main traverse was made, the unaltered beach sand contains about 0.28 per cent. ferric oxide, usually in the form of a yellow-brown coating to the silica grains; shell fragments are also present. The amount of shell varies considerably in samples taken from different areas of the beach. In the area of the beach near to the transect line along which the samples were obtained, the amount of shell grit present was small and was usually about 3 per cent. of the whole sample. In other parts of the beach the amount of shell debris is very much higher and one may get deposits of almost pure shell debris.

III. Climate

No suitable information is available for the rainfall of the Woy Woy district, but records from Gosford, which is a few miles to the north, are probably fairly well applicable to the area studied.

Data on the evaporation are more difficult to obtain and those in Table 1 are for the Sydney district, some 36 miles to the south. Although these latter figures are not directly applicable they may be taken as a guide.

TABLE 1

AVERAGE MONTHLY RAINFALL AND EVAPORATION (POINTS (= 0.01 IN.))

	Length of Record	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Annual
Rainfall														
Gosford	63 years	397	444	558	512	490	372	457	312	338	298	312	369	4858
Sydney	73 years	360	424	500	553	519	481	490	290	279	288	280	286	4750
Evaporation														
Sydney	71 years	553	425	367	267	185	150	156	200	274	388	426	568	3939

It will be seen that for 6 months the average evaporation either exceeds or approximately equals the precipitation. In view of the very porous nature of the sands, however, even in these months it is probable that more of the rain would be lost by drainage through the soil than by evaporation following capillary rise. In the other months the net movement of water in the profile will clearly be downward.

IV. Distribution of Soil Types and Vegetation

A survey of the area shows that the soils may be grouped under four headings. The distribution of these soils is shown in Figure 1. Nearest to the beach is a zone of undifferentiated sands about 200-300 yd. wide. Further from the beach is the main zone of iron podzols with the differentiation of soil horizons becoming more marked away from the beach. Near Woy Woy is an area with well-defined humus podzols. In addition there are the characteristic swamp soils associated with the small lagoons and swamps, which lie between some of the major sand ridges. These swamp areas have not been included in the present investigation.

The vegetation of the area varies in a similar way to the soils. At the beach front there is the typical flora of dune colonizers, giving place to a *Leptospermum laevigatum* F. Muell.-*Banksia integrifolia* L.f. thicket about 100 yd. wide. Isolated trees of *Eucalyptus botryoides* Sm. begin to occur about 150 yd. from the beach and increase in number to form with *Angophora intermedia* DC. a fairly open woodland, which covers the area occupied by the iron podzols. Where the humus podzols occur, *Angophora intermedia* is replaced by *A. lanceolata* Cav. The swampy areas between the sand ridges bear all stages in the succession from open water with *Typha* to *Melaleuca viridiflora* Gaertn.

V. Development of Soil Profile

In order to follow the development of the soil profiles a series of samples were taken along a transect line running parallel to the road from Ocean Beach to Woy Woy. Pits for sampling the soil profiles were dug on the tops of the ridges in order to avoid confusion with the complex soils associated with the

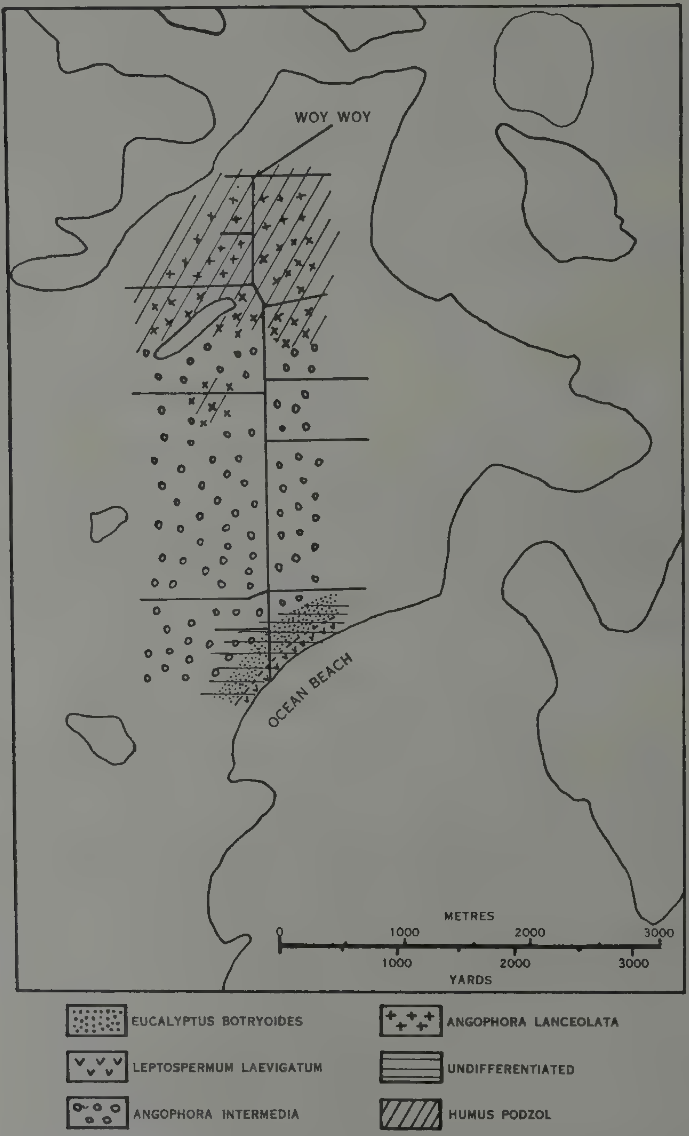
WOY WOY
OCEAN BEACH
METRES
0
1000
2000
3000
1000
2000
3000
YARDS
EUCALYPTUS BOTRYOIDES
ANGOPHORA LANCEOLATA
LEPTOSPERMUM LAEVIGATUM
UNDIFFERENTIATED
ANGOPHORA INTERMEDIA
HUMUS PODZOL

Fig. 1.—Sketch map of the area studied showing the distribution of the vegetation and the soil types. The zone between the undifferentiated soils and the humus podzols is occupied by iron podzols. Compare with aerial photograph in Plate 1.

swamps that often lie between the ridges. For samples from depths greater than 3 ft. a post-hole borer was used, enabling sampling from depths down to 7 ft.

Soil pH was determined with a glass electrode, using just sufficient distilled water to enable the electrode to be immersed easily in the sand. *Calcium carbonate* was estimated by adding a known quantity of 0.5N hydrochloric acid and back titrating the unused acid.

Ferric oxide. Iron was estimated colorimetrically as the thiocyanate. The value for total iron has been expressed as ferric oxide.

Organic carbon was estimated by the Walkely-Black method (see Piper 1944, p. 223).

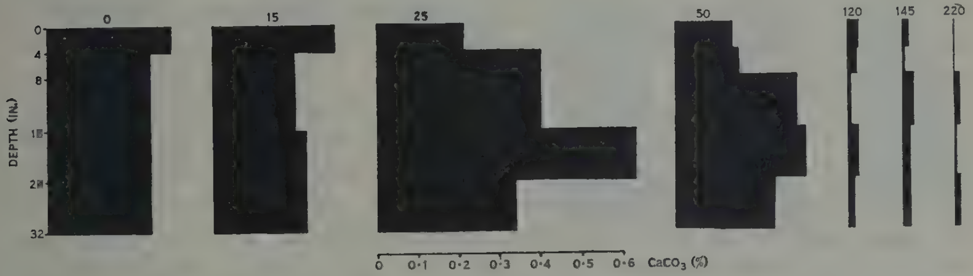

Fig. 2.—Histograms showing the amounts of calcium carbonate in the profiles. The figures above each histogram give the distance in yards from the beach.

(*a*) *Disappearance of Calcium Carbonate*

The distribution of calcium carbonate in the various profiles examined is shown by the histograms in Figure 2. In samples taken at 220 yd. or further from the beach front no appreciable amounts of calcium carbonate were detected. The small amounts shown at 220 yd. in Figure 2 are probably not calcium carbonate but exchangeable bases. Figure 4 shows the amount of calcium carbonate in the surface 0-4 in. This curve is comparable with that obtained by Salisbury (1925). If we accept the oldest ridges as being 4000 years old, then a period of about 200 years is required to remove all the calcium carbonate from the upper soil layers.

The amount of calcium carbonate in the sand of the present beach front varies greatly. Near Mt. Etalong shell grit forms more than half the beach material whereas at the point where the transect began there was only about 3 per cent. This variation from one part of the beach to another means that the figures for loss of calcium carbonate must be treated with some reserve because the amounts of shell grit in the older beaches may not have been similar to those in the present beach. At first sight the smoothness of the curve in Figure 4 might indicate a uniform parent material but the smoothness of the curve primarily reflects the rapidity of the leaching and there could have been considerable variation in the parent material without its being apparent in the shape of the curve.

There seems to be a surprising uniformity in the figures obtained by the various workers for the time taken to remove calcium carbonate by leaching. Salisbury found that in the Blakeney Point dunes, although the initial figure for the calcium carbonate was only 0.42 per cent., between 200 and 300 years were necessary for its complete removal from the dune surface, this being approximately the same as the figure for the Southport dunes, which contained 6.9 per cent. of calcium carbonate. Hissink (1938), studying the rate of leaching of the muddy deposits in the reclaimed areas in Holland, again obtained a figure of 200-300 years for the removal of the calcium carbonate, although the texture of the soil was markedly different.

It is often assumed that the major factor in the removal of the calcium carbonate is the movement of carbon dioxide-charged rainwater through the soil. However, attempts to follow the removal of the calcium carbonate by allowing water with dissolved carbon dioxide to percolate through columns of sand or to calculate the probable rates of solution based on rainfall and evaporation data (e.g. Jenny 1941*a*) tend to be very misleading. Under field conditions two additional factors play an important part in the process. Firstly, the accumulation of organic matter in the soil and the subsequent production of organic acids due to microbiological activity will tend to increase the rate of removal. Secondly, there is a considerable return of bases, and particularly calcium, to the upper layers of the soil in the fallen plant material; this will lead to a slower net rate of calcium loss than might otherwise be expected. At present it is impossible to say what the effect of these two opposing factors is and how this in turn modifies the normal leaching process.

(*b*) *Soil Reaction*

The unchanged beach sand has a pH of 8.8. As the calcium carbonate disappears the pH falls and at 220 yd. from the beach, where there is no longer any calcium carbonate, the pH is 6.1. The reaction of the lower layers of the soil follows closely on that of the surface.

Beyond 220 yd. the general drift in pH is downwards to 5.5. At about 2750 yd. the pH falls rapidly to 4.5. This change is correlated with the change in dominant tree from *Angophora intermedia* to *A. lanceolata.*

(*c*) *Soil Organic Matter*

The beach sand contains only small amounts of organic carbon. As is shown in Figure 5, the amount in the surface 4 in. increases rapidly during the first 100 yd. until it reaches a value between 0.5 and 0.6 per cent. At this value the accumulation and decomposition of organic matter are roughly in equilibrium. In the oldest ridges with humus podzols the amount of organic carbon rises to 0.8 per cent.

(*d*) *Movement of Iron*

Histograms showing the amount of iron in the upper 32 in. of selected profiles are given in Figure 3. The interpretation of the results of the analyses for iron presents several difficulties. Although sands near to the beach front seem to be fairly uniform in their iron content, it is most unlikely that a similar uniformity initially existed throughout the whole of the area of the sand ridges. Any interpretation based on the absolute amounts of iron present is therefore subject to considerable error. Reference to the histograms in Figure 3 shows that the amount of iron in the profile is appreciably less at 220 yd. than at 145 yd., which might suggest that leaching had occurred, and that the iron was being deposited lower down in the profile. Numerous holes were sunk to the depth of 7 ft. but no evidence of any deep-seated zone of accumulation was found. That leaching should occur so uniformly throughout the profile is most improbable. A more likely explanation of the differences in the amounts of iron found is that the sands forming the different ridges initially had appreciably different iron contents. Analyses of samples from depths of 6 or 7 ft., that is, well below the region of horizon development, all gave about 0.28-0.30 per cent. iron. This uniformity seems to indicate a redistribution of iron by ground water rather than reflecting any original uniformity in iron content. An examination of the distribution of iron throughout numerous profiles shows that there is no clear evidence of iron accumulation until the profiles at 280 yd. are reached.

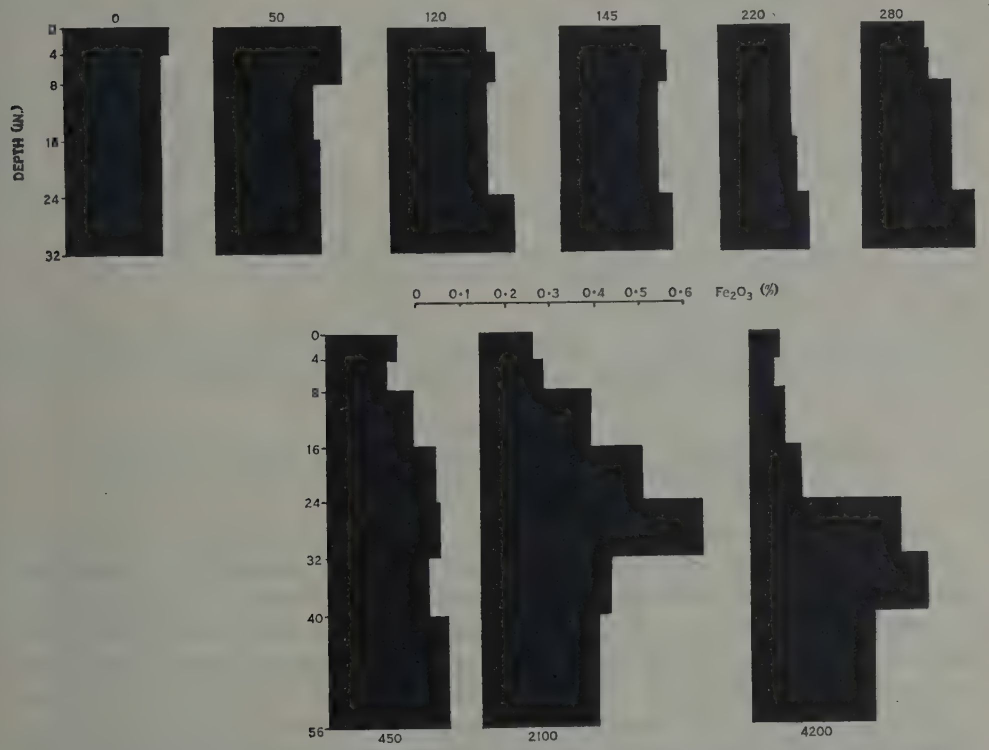

Fig. 3.—Histograms showing the amounts of iron in the profiles expressed as Fe_2O_3. The distance in yards from the beach of each profile is given.

The profile at 280 yd. showed some visual indication of horizon development in the field, the upper 8 in. of the profile being distinctly less yellow than the lower layers. As one proceeds further from the beach the leached layer becomes progressively more marked and at 1000 yd. a distinct B horizon is visible. This begins at about 15-18 in. below the surface. The lower boundary of the B horizon is usually indistinguishable in the field in profiles from this region. From 1400 yd. onward, the B horizon is quite distinct, commencing at about 18-19 in. from the surface and extending downward to about 36 in. As the distance from the beach increases, the A horizon extends deeper into the soil and the B horizon also increases in depth. This is well shown in Figure 6.

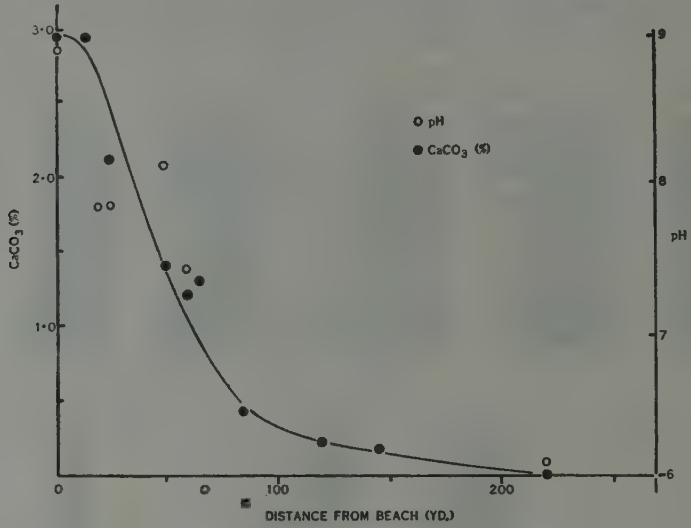

Fig. 4.—Relation between the amount of calcium carbonate in the surface 4 in. and the pH of the surface soil.

All the profiles beyond about 3000 yd. are those of typical humus podzols (cf. Fig. 7). These are clearly associated with the presence of *Angophora lanceolata.* Between 3000 yd. and the beach, *A. intermedia* is more prominent and the soils are typical iron podzols. There are, however, several somewhat isolated areas with *A. lanceolata* in the main iron podzol region—these have soils with a typical humus podzol B horizon. Reference to Figure 4 shows that in most soils between 300 and 2000 yd. the pH of the surface layer is approximately 5.5. These are nearly all typical iron podzols. Beyond 2000 yd. the pH of the surface layer falls to about 4.5 and humus podzols occur. The region between 2000 and 3000 yd. is the transition zone where *A. intermedia* is being replaced by *A. lanceolata.* Joffe (1936, p. 281) has pointed out that in view of Mattson's work on the fixation of humus by sesquioxides one would anticipate that a "higher pH should tend to form an iron ortstein, and a low pH, a humus ortstein." This would seem to be borne out by the present work.

VI. General Discussion

From the foregoing evidence it is clear that the sand ridges investigated show the progressive development of a typical podzol profile. The total length of the transect studied is approximately 4500 yd. and this may be taken as representing the amount of material accumulated since the ridge-building process began. If we take 4000 years as the time since the change in sea-level occurred and initiated the ridge-building then we may as a first approximation regard 1 yd. of the transect as representing the amount of sand accumulated in a year.

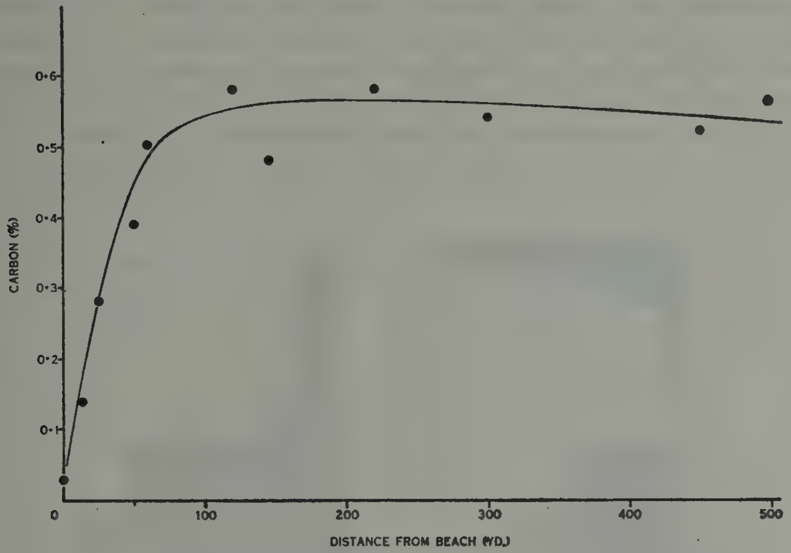

Fig. 5.—Relation between organic carbon in the surface 4 in. and the distance from the beach.

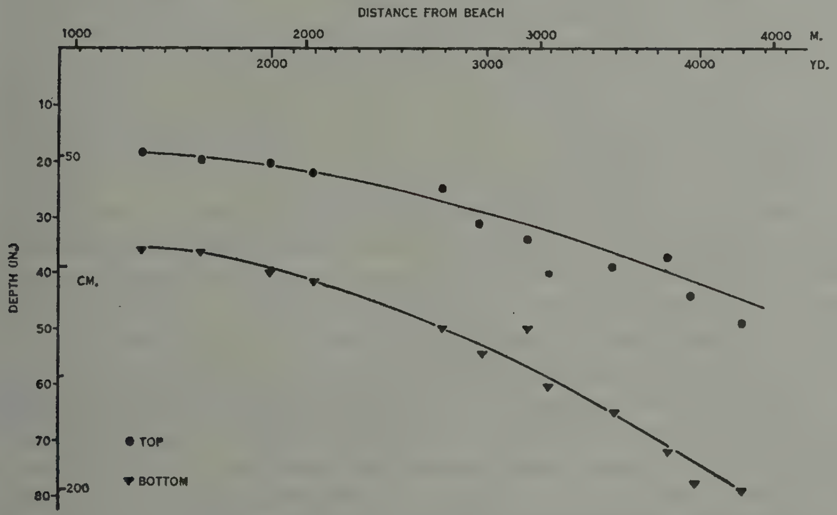

Fig. 6.—Increase in depth of the B horizon with increasing distance from the beach.

This then enables us to substitute "years" for "yards" in the various figures and to give the following account of the soil changes which have taken place.

The sand that formed the first ridges had a certain amount of calcium carbonate in the form of shell debris. At first this was removed rapidly and approximately half the calcium was removed in the first 50 years. After about 200 years all the calcium carbonate had gone. During this period the surface pH fell from 8.8 to about 6. As the pH fell below 6, leaching of iron began and in a further 50 or so years appreciable stratification in iron had occurred. The initial removal of iron was from the upper layers and at least part of the transported iron was deposited in the form of a B horizon at about 20-30 in. below the surface.

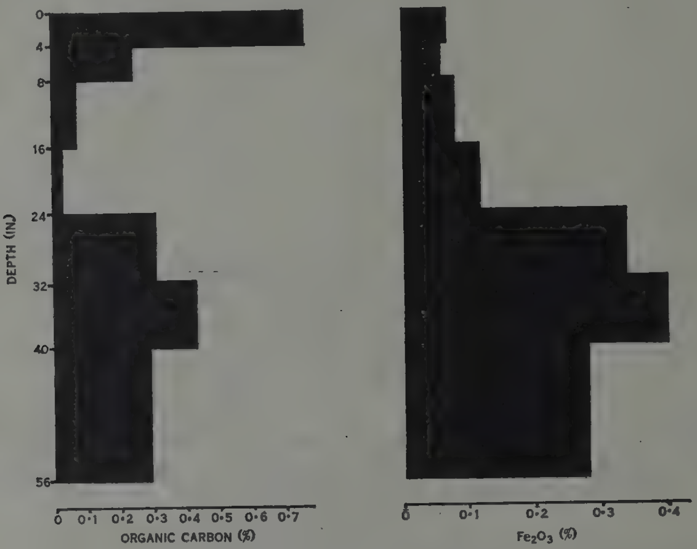

Fig. 7.—Histograms showing the distribution of organic carbon and iron in a humus podzol at 4200 yd.

After about 300 years, that is, about 100 years from when leaching of iron began, a profile was developed in which a distinct A horizon could have been seen in the field. By about 1000 years the B horizon had become fairly well differentiated, although in a profile of this age the lower boundary of the B horizon is very indistinct. In 2000 years the profile had developed all the characteristics of an iron podzol with well-marked A_1 and A_2 horizons and a pronounced B horizon extending from about 20 to 40 in. below the surface. With increasing age the B horizon moved slowly downward. At some stage the iron podzol changed to a humus podzol. The change is correlated with the replacement of *Angophora intermedia* by *A. lanceolata* as one of the dominant trees. This change seems to have occurred about 2500-3000 years after the ridges were formed in most cases, but the occurrence of isolated humus podzols associated with *A. lanceolata* on ridges which are much less than 3000 years old strongly suggests that the appearance of *A. lanceolata* initiates the formation of the humus podzol. The association of such a marked difference in soil type with the occurrence of a particular tree species is by no means unique. There is for example the development of the striking "egg-cup" podzols beneath individual trees of kauri (*Agathis*) in New Zealand (cf. Leeper 1948, p. 46).

Maze (1941), in writing of the profiles of the Tomago sand beds, considered that the development of humus podzols was associated with a ground water-table. In an attempt to investigate such a suggestion a series of holes were sunk across the sand ridge at 4200 yd. These holes showed clearly that the B horizon followed roughly the ground surface except that on the slopes of the ridge the depth of the B horizon increased somewhat. It is possible that this may have been due in part to surface erosion of the top of the ridge. On the crest the B horizon began at 49 in. from the surface; on the side of the ridge approximately 5 ft. below the crest the B horizon began at about 60 in. The relation of the B horizon to the curved crest of the ridge makes it fairly clear that the humus horizon cannot be associated directly with a standing water-table. This was confirmed during July 1949, when there was a marked water-table at about 7 ft. below the average ridge crests. In the centre of the ridges the B horizon was about 2 ft. above the water-table while on the slopes of the ridges it was a similar distance below. It seemed therefore that there was no simple relationship between this water-table and the B horizon.

In the present work there is clear evidence of increase in depth of the A horizons with age and the gradual movement of the B horizon downwards. This evidence is based partly on analyses for iron and partly on field measurements in which the B horizon was identified by its colour and texture. Aaltonen and Mattson (cf. Jenny 1941*b*, p. 41) consider that in podzols the B horizon grows from the bottom up. Even if due allowance is made for discrepancies that might arise by taking measurements from the visual upper boundary of the B horizon rather than the point of maximum sesquioxide accumulation, it is still difficult to see how the evidence from the Woy Woy sands could be reconciled with the schematic picture of Jenny. Further evidence, however, is required on this point.

The soils studied form a well-defined suite, which provides an excellent opportunity for the study not only of the pedological processes involved but also of the associated ecological problems.

VII. Acknowledgment

The authors wish to acknowledge the assistance of a grant from the Commonwealth Research Fund.

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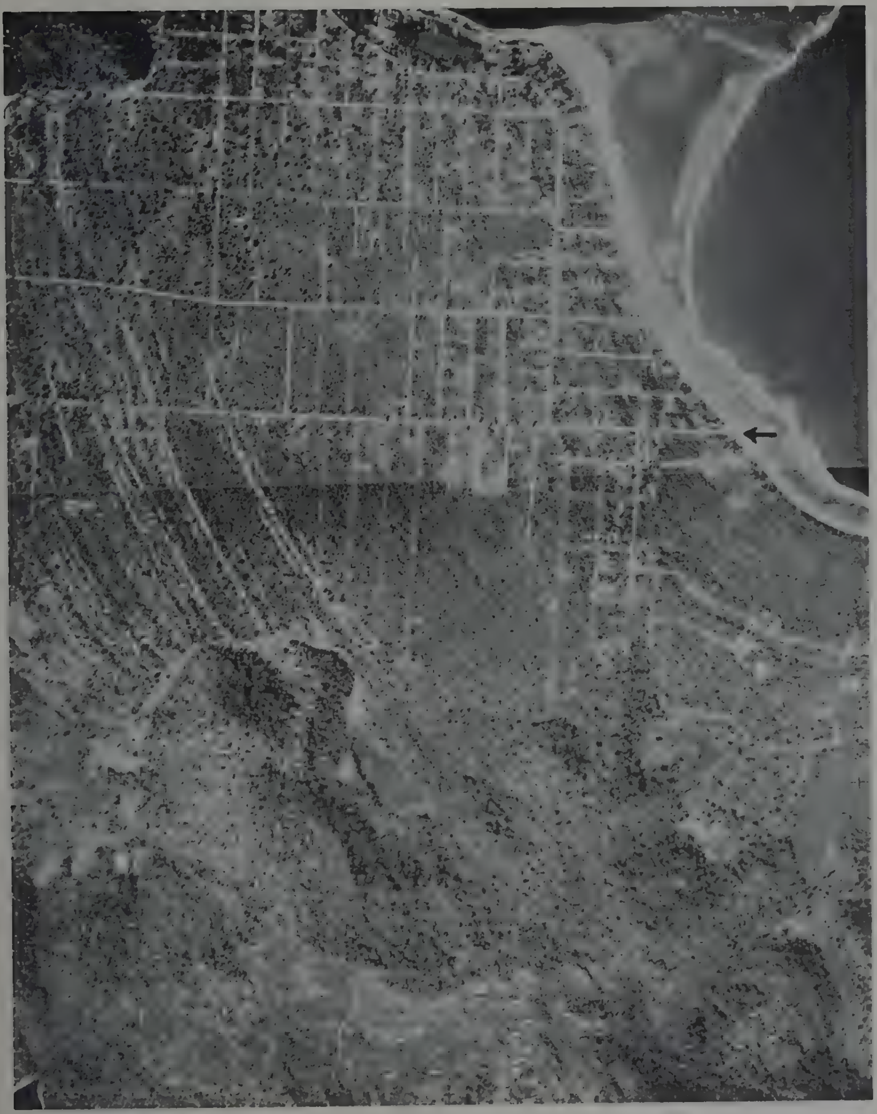
RATE OF PODZOL DEVELOPMENT IN SANDS



Aerial photograph of part of the area investigated. The parallel sand ridges show clearly in the upper part of the photograph. The road along which the soil pits were dug is indicated by the arrow. The photograph does not take in the area of the humus podzols. (Published by permission of Adastra Airways.)

THE BIOLOGY OF *HYPERICUM PERFORATUM* L. VAR. *ANGUSTIFOLIUM* DC (ST. JOHN'S WORT) IN THE OVENS VALLEY, VICTORIA, WITH PARTICULAR REFERENCE TO ENTOMOLOGICAL CONTROL

By Nancy Clark*

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Summary

A study of the biology of *Hypericum perforatum* L. var. *angustifolium* DC in the Ovens Valley, Victoria, has shown that the weed possesses characteristics that make it a difficult species for effective entomological control. They include the ability to prosper under a diversity of environmental conditions after successful establishment from seed; a great capacity for vegetative reproduction by suckering; and the delayed germination of a proportion of the seed for at least 6 years, probably owing to the presence of an inhibitor in the sticky exudate of the seed capsule. The problem of control is made more difficult by the unfavourableness of a large part of the area for the growth of other herbaceous plants capable of competing effectively with either mature *Hypericum* or its seedlings.

The leaf-eating beetles *Chrysomela gemellata* Rossi and *C. hyperici* Forst. differ greatly in their ability to destroy well-established stands of the weed. The susceptibility of mature *Hypericum* to defoliation depends on environmental conditions, e.g. the physical condition of the soil, which determine the life span of the individual crown and the rate and amount of vegetative reproduction. *C. hyperici* is highly destructive only in stands characterized by large crowns and limited vegetative reproduction; whereas *C. gemellata* can eliminate any type of stand occurring in treeless areas. The difference between the insects is due to the fact that *C. gemellata* can sustain the process of defoliation much longer than *C. hyperici.*

It so happens that environmental conditions most favourable for the initial multiplication of both insects occur in the very sites in which the weed is most readily controlled, i.e. where the established plants are of the type most susceptible to insect attack, and where seedling regeneration is most likely to be suppressed by the associated flora.

The stands of *Hypericum* that occur in areas less favourable for the initial colonization by the insects are generally more resistant to defoliation. Some of these stands, e.g. those present in eucalypt forest, cannot be destroyed by hand defoliation sustained for longer periods than the insects can maintain the process. Frequently, plants capable of ousting mature wort damaged by insect attacks or of suppressing seedling regeneration are scarce or absent, e.g. many areas of gold dredgings. Consequently, if the insects do succeed in destroying the original stands in such sites, the weed has a good chance of successful regeneration from seed. In many such areas in which the weed was destroyed in 1946 or 1948 St. John's wort is already re-established as the predominant plant. It has either achieved its former density or is well on the way towards doing so.

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* Division of Entomology, C.S.I.R.O., Field Station, Bright, Vic.

I. INTRODUCTION

Some years ago, the leaf-eating beetles *Chrysomela gemellata* Rossi and *C. hyperici* Forst. were liberated in Australia with the object of controlling *Hypericum perforatum* L. var. *angustifolium* DC, St. John's wort (see Wilson and Campell 1943). The insects were first established near Bright in the Ovens Valley, Victoria. Between 1940 and 1947 they were responsible for the destruction of dense infestations of the weed extending over a total area of several hundred acres. The results were so interesting that it was decided to investigate the ability of the insects to control the weed in the Bright district. The necessary studies were carried out during 1948-1951 by Mr. L. R. Clark and the writer. This paper deals with aspects of the ecology of the plant and those of its characteristics relevant to an understanding of the effects of the defoliating insects.

The nature and degree of control given by insects after their establishment and multiplication could depend not only on their habits but also on the characteristics of the host plant and the associated flora. Environmental factors could influence the effectiveness of the insects by determining the extent and speed of recovery or re-establishment of the weed after severe damage or destruction.

II. THE ENVIRONMENT OF THE WEED

(*a*) *General Description*

Recent estimates of the extent of the St. John's wort infestation in Victoria by the State Lands Department (unpublished) indicate that the weed occurs over approximately 116,000 acres, of which 61,000 are heavily infested, 29,000 fairly heavily infested, and 26,000 lightly infested. The total is much lower than the estimate of 250,000-400,000 acres given by Currie and Garthside (1932) and, later, by Cashmore and Campbell (1946). Approximately 75 per cent. of the total infestation, including 53,000 acres of heavily infested land, occurs in the Bright and Myrtleford districts in north-eastern Victoria.

The principal area of infestation is situated in and near the valley of the Ovens River and its tributaries between Harrietville and Myrtleford, 35 miles downstream. Then mean annual rainfall increases from 34.4 in. at Myrtleford to 54.9 in. at Harrietville, 63-65 per cent. falling between May and October. The winters are cold, with frequent and severe frosts, and the summers warm, although maximum temperatures rarely exceed 100°F. The climate becomes warmer and drier as the valley widens below Myrtleford; and cooler and wetter east of Harrietville where the land rises steeply to Mt. Hotham and the High Plains (altitude 6,000 ft. approx.). The weed assumes pest proportions in areas with altitudes up to 2,000 ft. and mean annual rainfalls exceeding 30-35 in. (see also Moore and Cashmore 1942).

The original vegetation consisted of eucalypt forest on the hills and eucalypt forest or woodland in the river valleys. The characteristic trees, shrubs, and grasses are listed in Table 1 (see also Ewart 1910). During the latter half of the 19th century thousands of temporary settlers entered the area and engaged in various forms of gold mining (digging, sluicing, dredging, etc.). Most of the timber in the valleys and on the nearby hills was removed, and the dredges reduced some thousands of acres of river flats to a rubble of coarse sand, gravel, and rocks. St. John's wort was first established at Bright about 1875, and by 1900 had entered most of the areas where it is now present. The removal of the natural vegetation was undoubtedly responsible for the rapid spread of the weed, the seed being carried by stock and readily established wherever the original plant cover was destroyed.

TABLE 1

PLANTS PROMINENT IN THE FORESTS AND WOODLANDS OF THE BRIGHT DISTRICT (ALTITUDES 900-2,000 FT.)

A. Hillsides

(i) Northerly and westerly aspects

Trees: *Eucalyptus cordieri* Trabut, *E. dives* Schauer, *E. maculosa* R.T.Baker, *E. macrorrhyncha* F. Muell., *E. radiata* Sieb., *E. polyanthemos* Schauer

Other species: sclerophyllous shrubs (legumes, epacrids, etc.), *Poa caespitosa* Forst., *Danthonia pallida* F.Muell., *Themeda australis* (R.Br.) Stapf., *Danthonia* sp.

Note. Cover near ground surface frequently very sparse

(ii) Southerly and easterly aspects

Trees: *Eucalyptus radiata, E. mannifera* (A.Cunn. Herb.) Mudie, *E. maculosa, E. dives, E. bicostata* Maiden, Blakely, and Simmons, *E. chapmaniana* Cameron

Other species: sclerophyllous shrubs, including larger species than in (i); *Poa caespitosa, Themeda australis*

Note. Cover near ground surface usually very dense

B. Floors of valleys

Trees: *E. mannifera, E. stuartiana* F.Muell., *E. camphora* R.T.Baker, *E. viminalis* Labill., *E. pauciflora* Sieb., *E. stellulata* Sieb., *E. camaldulensis* Dehn., *Acacia* spp.

Other species: sclerophyllous shrubs, *Themeda australis, Poa caespitosa, Danthonia* spp., *Microlaena stipoides* (Labill.) R.Br., *Eragrostis* sp.

Note. Cover near ground surface usually dense

With the decline in mining activity the valleys were settled by farmers who now engage in dairying, grazing sheep and beef cattle, and growing apples, walnuts, tobacco, vegetables, and fodder crops. Over the last 30-40 years eucalypt forest has developed again on the hillsides, and some dredgings have been occupied by a dense scrub of eucalypts and acacias. Extensive areas on the hills and some dredgings have been planted with *Pinus* spp.

The infestation is largely confined to altitudes below 2,000 ft. In the wet sclerophyll forests and alpine woodland above this level the weed is very dense along stock routes leading to the High Plains east of Mt. Hotham, and occurs in patches around mine workings and on roadsides. The highest altitudes at which *Hypericum* has been found are 4,500 ft. on Mt. Buffalo, and 5,000 ft. near Mt. St. Bernard, where it was recorded by Ewart and Tovey in 1909 and still persists as a small patch. The absence of the weed in alpine meadow (5,000-6,000 ft.), which is grazed heavily by cattle in summer, is attributed to temperatures too low for seed germination or seedling survival (see Section IV (*b*)). Below 2,000 ft. *Hypericum* is consistently absent only on the dry aspects of the steeper hills, where the soils retain insufficient moisture for its successful establishment. The failure of the infestation to spread downstream beyond Myrtleford is probably due primarily to the relatively low rainfall in this vicinity. Within the main infestation area the distribution and abundance of *Hypericum* are determined by land use.

(*b*) *Distribution in Relation to Land Use*

Extensive surveys during 1948-50 showed that by far the larger part of the present infestation occurs on timbered land and dredgings. The original infestation on cleared land has been steadily reduced over the last 30-40 years by a change in farming practice, aided in recent years by the activities of the chrysomelids. The distribution and abundance of *Hypericum* in these three main classes of habitat are discussed below.

(i) *Timbered Areas*

Eucalypt forest.—Hypericum became established in these forests when the original timber was felled to provide fuel for dredges etc. Disturbance still occurs to a variable extent as a result of fire, timber cutting, and grazing, and the density and vigour of the weed depend apparently on the amount of damage caused to other plants, particularly the perennial grasses *Poa* and *Themeda*. The weed maintains itself and spreads by suckering, and even where the ground cover attains its maximum density, as in sites undisturbed for 15-20 years, *Hypericum* is present. Much of the forest on the lower hill slopes adjoining the valleys has been cleared in recent years by farmers preparing the land for grazing or cultivation. Their practice of ringbarking or felling, followed by burning, favoured the growth and rapid spread of *Hypericum,* and much of the land involved was abandoned. It is now occupied by dense stands of the weed growing in association with bracken (*Pteridium aquilinum* Kuhn), sapling eucalypts, and acacias.

Pine plantations.—The replacement of natural forests by pines provides, in its initial stages, excellent conditions for the establishment of dense stands of wort, which are reduced as the pine canopy increases, and finally eliminated when the canopy cuts off all direct sunlight. As the pines age, or are thinned or pruned, and the canopy becomes less dense, seedlings of *Hypericum* become established. When the pines are felled this nucleus of wort expands rapidly, and in a few years a dense stand developed from both suckers and seedlings is present again. *Hypericum* is generally the last plant to be excluded by the pines and the first to reappear.

(ii) *Dredgings*

Hypericum is undoubtedly the most successful pioneer species on the rubble of sand and stones that remains after dredging, and recently dredged areas are occupied mainly by St. John's wort and other weeds. On many of the early dredgings acacias and eucalypts have become dominant (*Acacia dealbata* Link., *A. decurrens* Willd., *A. mollissima* Willd., *A. pravissima* F. Muell., *Eucalyptus mannifera, E. stuartiana, E. stellulata,* etc.). The vegetation on dredgings has the appearance of a succession beginning with a community of weeds, and ending with a community dominated by *Eucalyptus* spp. *Hypericum* is present as a very abundant species in most communities. It usually persists as the predominant herbaceous plant, except where acacias and large shrubs (principally *Leptospermum* and *Kunzea* spp.) form a closed stand.

(iii) *Cleared Land*

Grazing land.—Much of the better-class grazing land has been sown with introduced perennial grasses (*Lolium perenne* L., *Phalaris tuberosa* L.) and legumes (*Trifolium subterraneum* L., *T. repens* L., *Medicago sativa* L.). *Hypericum* is frequently abundant in newly sown pastures, particularly where the land has been inadequately cultivated before sowing or where rabbits are numerous. On well-established pastures that have been fertilized and intensively grazed for some years the weed is practically absent, although it is commonly found in pastures regularly cut for hay. *Hypericum* is very rare in pastures dominated by *T. subterraneum* and annual grasses (*Vulpia bromoides* (L.) S.F.Gray, *Bromus* spp.) that have developed where the clover has been introduced without cultivation. The weed is also uncommon in pastures composed almost entirely of annual grasses and herbs, which are the product of continuous and heavy grazing.

Hypericum of varying density and size occurs in native perennial grass pastures in which the following species are either dominant or common: *Danthonia* spp., *Themeda australis, Poa caespitosa, Microlaena stipoides,* and *Eragrostis* sp. In most instances these pastures are grazed by beef cattle, which are sent to mountain leases during the summer. The weed is comparatively rare where such pastures are grazed throughout the year. The available evidence suggests that the proportion of St. John's wort to perennial grasses depends to a considerable extent on seasonal conditions and management. The latter frequently favours the weed, e.g. some *Themeda* pastures are burned regularly.

On grazing land, which includes the greater part of the area cleared of the original infestation, it is believed that defoliation (by stock or by the chrysomelids) or cultivation has been the primary cause of the destruction of the weed. The role of the pasture species has been that of providing sufficient grazing to enable defoliation of the weed without serious damage to stock (Dodd 1920), and preventing re-establishment of the weed from seed. The annual winter-growing legume, *Trifolium subterraneum,* which is one of the most productive pasture species under intensive grazing, and easily and cheaply established, has undoubtedly played a major part in the suppression of *Hypericum.*[*]

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[*] *Hypericum* is able to maintain itself in very dense swards of *T. subterraneum* that are either lightly or intermittently grazed, or regularly cut for hay. It has been observed that mature plants of *Hypericum* frequently develop more growth early in the autumn than the clover, and many of the procumbent stems remain above the clover during the winter. The erect fertile stems also escape shading by the clover unless defoliation occurs (cf. Moore and Cashmore 1942).

Only two species, the perennial grasses *Hemarthria uncinata* R.Br. and *Themeda australis*, are known to have invaded and destroyed established stands of St. John's wort. The former is a coarse summer-growing species occupying limited areas on sandy river flats and is unattractive to grazing animals. The latter is successful only where grazing by stock or rabbits is very light (see also Davey 1919). It has been observed that mortality in *Hypericum* occurs mainly in the autumn, suggesting that it is finally due to the accumulation of grass leaves etc., which greatly reduces the light available to the young shoots of plants weakened by competition for moisture during the summer.

Cultivated land.—Stands of *Hypericum* are readily destroyed by deep ploughing followed by sufficient cultivation to prevent the establishment of suckers or seedlings. Thus the weed is rare or absent where crops requiring frequent cultivation are grown, e.g. tobacco or vegetables. The densest stands of *Hypericum* are found on abandoned arable land. Soon after cultivation ceases such areas are occupied by a dense growth of wort seedlings. In approximately 3 years the weed is usually sufficiently well grown to exclude all species except small annuals and mosses. Ultimately, some stands are invaded by perennial grasses etc., but the process of replacement is a very slow one and rarely leads to the complete exclusion of *Hypericum*. In one observation area, ploughed 12 years ago, only annuals are present with the weed. In another, ploughed 15 years ago, *Themeda* has become prominent and the present vegetation consists of alternes dominated by *Themeda* or *Hypericum*.

(*c*) *Influence of Habitat on the Growth and Vegetative Reproduction of* Hypericum

The success of St. John's wort in its new environment must be attributed to its reproductive capacity. It not only has a very high seed production per plant but also is capable of vigorous vegetative reproduction. Reproduction by seed was responsible for its rapid spread initially, when man provided the conditions necessary for successful seedling establishment (see above and Section IV (*a*)). Its capacity for vegetative reproduction enables it to persist and spread in areas where these conditions no longer prevail. This characteristic was of special importance in the present study, as the resistance of stands to the attacks of the defoliating insects was determined largely by the rate at which vegetative reproduction occurred.

Stands of *Hypericum* are maintained by vegetative reproduction. A single plant may be represented by one or more crowns attached to the one system of vertical and lateral roots. In the late summer or autumn these crowns produce non-reproductive procumbent stems, which die off in the spring. Erect fertile stems produced towards the end of winter flower in late spring or early summer, and die off in the autumn. In the spring and autumn new crowns may be produced by adventitious shoots from the lateral roots. Development of roots from the procumbent stems in close contact with the soil may also occur. With the decay of the connecting root or stem tissue an independent root system is developed and new plants are produced. Because of the obvious difficulty of recognizing a plant, the crown has been used as the unit of measurement in the field studies described in this paper.

It was indicated in an earlier study (Clark and Clark 1952) that susceptibility to defoliation was related to the age composition of the crowns in a stand, which was influenced by soil conditions. Further evidence supporting this conclusion was obtained from observations made over a much wider range of vegetation-soil complexes in the Bright district. The life span of a crown and the extent of suckering are associated with the physical condition of the soil. Where conditions favour the development of deep vertical roots the crowns live for some years before vegetative reproduction occurs. The death of such crowns appears to be due primarily to intrinsic factors associated with aging. In shallow or stony soils, and in the presence of the competing root systems of other plants, the life span of the crowns is much shorter and suckering is an almost continuous process.

Two principal types of wort stand may be recognized:

(1) Stands in which the individual crowns are well spaced (approximately 0.5-1.5 per sq. lk.), the majority being large, 3 or more years old, and bearing relatively large numbers of stems. Frequently the crowns die out in small patches, and occasionally *en masse,* before much suckering occurs. The associated flora consists mainly of small annuals and mosses. Such stands have developed on arable land and on dredged areas in which a considerable amount of sandy soil remains in addition to gravel and rocks.

(2) Stands with smaller crowns in which the density ranges from approximately 0.5 per sq. lk. on the stoniest dredgings, and in some well-grassed areas, to over 5.0 per sq. lk. on shallow soils and in certain perennial grass pastures. In such stands the stems borne by the crowns are fewer and smaller than in (1), few crowns are more than 3 years old, and young suckers are always present and numerous throughout. The extreme example of this type occurs in areas of eucalypt forest. There, suckering is often so vigorous that a plant is rarely represented by a single crown. Frequently 10 or more crowns are attached to the same root system.

In the second type of stand, the stimulus to suckering seems to be provided by unfavourable circumstances such as a limitation of carbohydrate synthesis resulting from defoliation or shading, or by obstruction of the vertical root system. Evidence on the effect of the latter was obtained from an experiment at the Bright Field Station. In September 1950 seeds of *Hypericum* were sown in small plots distributed randomly over a patchwork of stony and deep soils, produced from the same parent material. Late in the autumn of 1951 the resulting plants were dug out and examined for suckers. All individuals grown on soil free from stones to a depth of 1 ft. or more possessed a well-developed vertical root system and no suckers. In those that had developed in soils with stones within 3 in. of the surface the main vertical root branched about 2-3 in. below the soil surface and the well-developed lateral roots bore one or more suckers.

III. The Effect of Complete Defoliation of Hypericum

(*a*) *Defoliation by Insects*

During the course of investigation, the effects of complete defoliation of *Hypericum,* maintained for varying periods, were observed over a wide range of habitats, wherever *Chrysomela gemellata* or *C. hyperici,* or both, were present in sufficient numbers. In a number of study areas changes in the status of the weed, attributable to defoliation, were measured quantitatively in terms of bulk yield and crown density. Estimates of yield were obtained for three large study areas (5-20 ac.) by a rating method. First, the infestation in each area was classified into a number of stand types. The study areas were then divided into strips (0.5-1.0 ch. wide), and the wort was classified into types at intervals of 2 yd. along a traverse 1 yd. wide passing through the middle of each strip. Each infestation was mapped in terms of stand types at the end of the spring growing period. The quantity of wort present was estimated from 10 samples (3 by 3 lk.) of each type, air-dried to approximately constant weight. An estimate of the dry weight of *Hypericum* per acre was obtained for the year prior

Table 2

EFFECT OF DIFFERENT PERIODS OF DEFOLIATION ON THE AMOUNT OF ST. JOHN'S WORT PRESENT AT THE END OF THE GROWING SEASON — DATA FOR THREE STANDS DEFOLIATED IN 1948 FOR THE FIRST TIME

Study Area	*A.* Arable Land, Clay Loam Soil Stand Approx. 12 Years Old			*B.* Arable Land, Deep Sandy Soil Stand Approx. 8 Years Old			*C.* Dredgings		
Period of Complete Defoliation	Approx. Area Sampled (ac.)	Amount of Weed Present* (cwt./ac. air-dry wt.)		Approx. Area Sampled (ac.)	Amount of Weed Present* (cwt./ac. air-dry wt.)		Approx. Area Sampled (ac.)	Amount of Weed Present* (cwt./ac. air-dry wt.)	
		Jan. 1948	Jan. 1949		Jan. 1948	Jan. 1949		Jan. 1948	Jan. 1949
Early September to late November	1·8	15·5	0·1	0·8	28·0	0·2	8·0	7·2	0·1
Mid October to late November	5·4	17·2	3·4	0·4	26·8	1·0	1·5	7·9	1·8
Mid November to early December	2·2	18·1	11·1	1·1	21·7	3·8	—	—	—
Undefoliated weed	5·4	17·1	20·3	1·7	26·2	12·1	7·5	7·7	5·5

* For undefoliated stands this represents the total seasonal yield of the erect fertile stems.

to defoliation and for the year when defoliation occurred. The limits of areas defoliated by larval and adult chrysomelids were mapped several times each year. Permanent strip transects 1 lk. wide and 1-20 ch. long (depending on the size of the study area) were used to measure changes in the crown density of *Hypericum* and the cover provided by the associated species (see Clark and Clark 1952) in each of these areas. The changes in crown density following defoliation in different types of wort stand were also studied in a number of small plots, 0.25-1.0 sq. ch. in area, distributed throughout the Bright district. These were sampled with a 1 by 1 lk. frame, by taking 100-500 random quadrats per plot, the number depending on plot size and uniformity. The number of wort crowns and the presence of other species were recorded for each quadrat.

The yield data obtained from the three large study areas are given in Table 2. These areas contained a representative sample of the *Hypericum* stands destroyed or severely damaged by the insects. On half of study area *A*, *T. subterraneum*, *Hypochoeris radicata* L., and annual grasses provided a fairly dense ground cover between the wort plants. On the other half the associated flora consisted of sparse annual grasses and herbs. The yield of *Hypericum* was much the same throughout the area. Study area *B* was occupied by a stand of large plants that were highly productive in 1947-48 but showed a marked decline in yield the following year, due apparently to uniform aging of the stand. Except for small patches of *Hemarthria* the cover provided by other species was negligible. Study area *C* included approximately equal parts of stony, recently dredged land, bearing wort and scattered acacias; and old dredgings, where more soil remained, bearing a community dominated by *Hypericum* and perennial grasses. The average yield of *Hypericum* was similar in each section, less than half that in study area *A*.

The insects stripped the plants of all leaves and the softer stem tissues, but plants which survived this attack made some regrowth during the 6 weeks or so of the growing period remaining after defoliation ceased. The immediate effects of the insect attack can be seen by comparing the amount of weed present on defoliated sites with the yield of similar unattacked stands. However, the yield of *Hypericum* in the following year was reduced significantly only where the crown density had been reduced very substantially. The weed recovered completely except where the mortality was high (see also Clark and Clark 1952).

Changes in crown density in a number of stands, following varying periods of defoliation in 1948 and 1949, are shown in Table 3. The well-established stands sampled included those on the three large study areas (A^1, A^2, *B*, and *C*), and a stand (*D*) at least 15 years old growing in association with a fairly dense cover of *Danthonia penicillata* (Labill.) F.Muell., which had been only very lightly grazed by sheep. These stands contained varying proportions of young and old crowns. The younger stands (A^3, A^4, A^5, and *E*) were all on sites similar in soil and topography to study area *A*. The cover of other species was sparse in all except *E*, which developed after the land was cultivated inefficiently and sown with perennial rye grass and subterranean clover.

TABLE 3

CROWN DENSITY OF ST. JOHN'S WORT BEFORE AND AFTER DIFFERENT PERIODS OF DEFOLIATION IN 1948 AND 1949 — DATA FROM PERMANENT TRANSECTS AND SMALL STUDY PLOTS

Habitat	Period of Defoliation	Crowns/Sq. Lk.		Size of Sample (sq. lk.)	Associated Species
		Before	After		
1948					
A^1. Arable land, clay loam soil (12 yr.-old stand)	Early September to late November	0·96	0·26	190	*T. subterraneum*, *H. radicata*
	Mid October to late November	1·46	1·30	600	*H. radicata*
A^3 As for *A*^{1} (3-4 yr.-old stand)	Early September to late November	1·37	1·11	100	Annual grasses and herbs
A^4 As for *A*^{1} (1-2 yr.-old stand)	Early September to late November	0·44	0·22	300*	Annual grasses and herbs
A^5 As for *A*^{1} (1-3 yr.-old stand)	Early September to late November	0·77 (+0·59 seedlings)	0·71	500*	Annual grasses and herbs
B^1 Arable land, deep sandy soil (8 yr.-old stand)	Early September to late November	0·87	0·06	320	Annual grasses and herbs
	Mid October to late November	0·95	0·08	120	Annual grasses and herbs
B^2 As for *B*^{1}	Mid October to late November	0·77	0·00	60	*Hemarthria uncinata*
C Dredgings	Early September to late November	2·78	0·47	600	*Poa caespitosa*, *Danthonia* sp., annual grasses and herbs
D Native perennial grass pasture, clay loam soil	Early September to late November	4·28	1·90	200	*Danthonia penicillata*, *T. subterraneum*, *H. radicata*
1949					
A^1 Arable land, clay loam soil (12 yr.-old stand)	May to Mid November	1·17	0·00	800	*T. subterraneum*, *H. radicata*
A^2 As for *A*^{1}	May to Mid November	8·23	0·00	500	Annual grasses and herbs
B^1 Arable land, deep sandy soil	June to Mid November	0·73	0·00	330	Annual grasses and herbs
E^1 Arable land, clay loam soil (2 yr.-old stand)	May to Mid November	1·59	0·00	100*	*Lolium perenne*, *T. subterraneum*
E^2 As for *E*^{1}	Early August to Mid November	1·13	0·61	100*	*Lolium perenne*, *T. subterraneum*

* Data from small study plots (*A*^{4} = 1 ac.; *A*^{5} = 2.5 ac.; *E*^{1}, *E*^{2} = 2 sq. ch.), the remainder from permanent transects.

In 1948 the longest period of complete defoliation was from early September until late November, and some plants survived in all stands. In the older stands (*A*^{1}, *B, C,* and *D*) the surviving crowns were of intermediate size and age, and the number remaining after 2-3 months defoliation depended on the proportion of very old and very young crowns present. Defoliation was most effective in the aging stand, *B*, which consisted almost entirely of old crowns and young suckers; and least effective in young stands (*A*^{3}, *A*^{4}, *A*^{5}) in which the majority of crowns were 1-3 years old. The shorter period of defoliation considered here (October to late November) destroyed only the most susceptible crowns.

In 1949 most stands were defoliated early in the winter, and wherever defoliation continued into November all crowns were destroyed. This early defoliation was due to *C. gemellata*. Eggs of this species begin hatching in late March or early April, whereas few *C. hyperici* eggs hatch before late July or August (see Clark 1953 for a detailed description of the seasonal occurrence of the insects). A direct comparison of winter-spring defoliation, and spring defoliation, was obtained only for the young stand, *E*, in which a high percentage of crowns survived the shorter period of defoliation. Observations were also made in two stands (not listed in Table 3) in which the process of defoliation was sustained from late May until early September only. In the first stand, which had developed in 2 years after the felling and removal of pine trees, a few very large plants were killed and, at the end of the growing season, the stand was practically indistinguishable in appearance from similar unattacked stands. The second stand was composed of large, old wort plants, all of which were killed.

None of the study areas provided any evidence that mortality in *Hypericum* was increased by the presence of competing species other than *Hemarthria* (*B*^{2}). This was not surprising for the annual species, which completed their life cycle when the moisture supply was still adequate, several weeks before *Hypericum* flowered. After they had dried off even the densest stands of *T. subterraneum* or *Vulpia bromoides* (the most abundant of the annual grasses) did not provide sufficient cover to shade completely the new shoots of *Hypericum* produced after defoliation ceased. Except for *Hypochoeris radicata* and *Rumex acetosella* L., which have a much shallower rooting system than *Hypericum* and provide cover near the ground surface only, perennial herbs were not abundant. The failure of the perennial grasses — *Danthonia penicillata, Poa caespitosa,* and *Microlaena stipoides* — to have any measurable effect might have been due to the fact that in their presence *Hypericum* suckers more vigorously (see Section II(*c*)). Thus these perennial grasses are probably associated with stands of *Hypericum* potentially more resistant to defoliation. The above species flower earlier than *Hemarthria* and *Themeda,* which make most of their growth in the late spring and summer and are more active during the period when defoliated *Hypericum* is recovering. Unfortunately, none of the plots containing *Themeda* was defoliated by the insects. However, observations elsewhere indicate that *Hypericum* growing in a fairly dense stand of *Themeda* is killed by a comparatively short period of complete defoliation in the spring. In the presence of *Hemarthria* or *Themeda* even partial defoliation has sometimes apparently "tipped the balance" in favour of the grasses and the wort has been destroyed. Elsewhere partial defoliation has had no effect.

These observations confirmed the previous conclusion that susceptibility to defoliation is related to age in *Hypericum* (Clark and Clark 1952) and indicated the importance of the length of the period of defoliation. They also showed the need for further study of the effect of different periods of defoliation and the presence of perennial grasses. As it was impossible to control beetle defoliation in particular areas for set periods, defoliation by hand was adopted.

(*b*) *Defoliation by Hand*

A suitable area for the hand defoliation experiment planned was found in a stand of weed that had occupied a gently sloping hillside after the land had been cleared of timber some 20 years ago. A range of types, classified on the basis of crown size and density and the presence or absence of *Poa caespitosa*, which was present in patches, was contained within the stand. An area of approximately 3 sq. ch. was selected, in which the following four types were present:

I. Small crowns at high density—only annual species present with the weed.
II. Small crowns at high density—*Poa caespitosa* present.
III. Large crowns at low density—only annual species present.
IV. Large crowns at low density—*Poa caespitosa* present.

In each type five lots of four contiguous plots were pegged, the boundaries being defined by cords. Each plot consisted of a central sampling area of 5 sq. lk. surrounded by a border strip 1 lk. wide. The weed in the border strip was treated in the same manner as that in the plot proper to avoid marginal effects. One of each set of four plots (allotted at random) was kept defoliated by hand for the following periods:

(1) April 26 to November 14, representing the maximum observed period of sustained defoliation over an extensive area by the larvae and adults of *C. gemellata* (6.5 months).

(2) August 22 to November 14, representing the maximum observed period of sustained defoliation over an extensive area by the larvae and adults of *C. hyperici* (2.75 months).

(3) August 22 to December 9 (3.6 months), an extension of (2) prolonging defoliation until general flowering of the weed had commenced.

(4) October 7 to December 9 (2 months), covering the period from the general emergence of adults of *C. gemellata* until flowering.

After the initial defoliation, when all leaves and soft shoots were removed (simulating, as closely as possible, the maximum degree of defoliation effected by the insects), all new shoots were removed at fortnightly intervals, the final defoliation occurring on the last date mentioned for each treatment. The material removed was air-dried and weighed. The number of crowns bearing live shoots was recorded for each plot on April 26, November 14, November 29, December 9, 1949, and February 10, 1950.

The four treatments could not be compared directly on the basis of percentage crown mortality, as defoliation stimulated suckering (see also Salisbury 1942). However, for practical purposes, it did not matter whether the survivors were individuals present at the beginning of the experiment, or new crowns. Consequently the treatments were compared on the basis of changes in crown density. The final count of crown numbers was made for each treatment on February 10, 1950, shortly after the beginning of the next growth cycle.

The significance of treatment differences was obtained by the analysis of covariance, taking the crown densities at the beginning and end of a particular period as the independent and dependent variables, respectively. In Table 4 the mean crown densities on 14.xi.1949 and 10.ii.1950 are expressed as proportions of the original mean densities (26.iv.1949).

The effects of the treatments varied with the type of stand, the differences being greater between plots of high and low crown density than between plots of similar crown density with or without perennial grass. In the high density types all treatments caused a decrease in mean crown density by mid November, the decrease being significantly greater under treatment 1. Differences between the other treatments did not become apparent until after defoliation ceased. In type I, treatments 1 and 3 were approximately equal in effect, and caused a significantly greater reduction than treatments 2 and 4. In type II, the final crown densities were relatively highest for treatment 2, and the other treatments did not differ significantly in effect. The different results of treatments 2 and 4 were probably due to the presence of *Poa*. The available soil moisture was adequate for both *Hypericum* and *Poa* until the end of November (November rainfall: 536 points; Meyer ratio 88). No rain fell in December until the last day of the month (50 points), and competition for moisture was probably severe. Plants that were able to make some regrowth in November (treatment 2) suffered less than those kept defoliated until the moisture supply was limited (treatment 4).

In the plots of low-density wort, treatment 1 caused a great decrease in crown numbers by mid November, when all crowns present in type III and 75 per cent. of those in type IV were recent suckers. Treatments 2 and 3 (equal at this time) destroyed a high percentage of the original crowns, but much suckering occurred. Few crowns were killed by treatment 4 which caused vigorous suckering, particularly in type III. Most of the crowns present on November 14 succumbed to the defoliation carried out on that date. At the end of the experiment the differences between treatments were not statistically significant in either type of stand. The relatively lower crown numbers in type IV, following treatments 2 and 4, again suggest that the presence of perennial grass affected survival.

As *Hypericum* reproduces so readily by suckering, particularly when damaged, the practical effect of defoliation depends not only on the mean reduction in crown density, but also on the distribution of survivors at the end of the period of defoliation. Unless extensive areas are left quite free of the

TABLE 4

RATIO OF NUMBER OF LIVE CROWNS AFTER DEFOLIATION TO NUMBER OF LIVE CROWNS BEFORE DEFOLIATION (MEANS OF FIVE PLOTS) IN FOUR STANDS OF *HYPERICUM* HAND DEFOLIATED FOR FOUR DIFFERENT PERIODS

	Type I—High Density, No Perennial Grass					Type II—High Density, *Poa caespitosa* Present				
	Defoliation Treatment*				Significance of Treatment Differences	Defoliation Treatment				Significance of Treatment Differences
	1	2	3	4		1	2	3	4	
No. crowns per sq. lk. 26.iv.1949	5·40	5·40	5·32	5·24		4·72	4·96	4·64	4·76	
Proportion present 14.xi.1949	0·36	0·94	0·73	0·84	$P<0\cdot05$	0·36	0·71	0·90	0·97	$P<0\cdot001$
Proportion present 10.ii.1950	0·07	0·34	0·06	0·30	$P<0\cdot05$	0·07	0·28	0·13	0·13	$P<0\cdot05$
No. of plots occupied 10.ii.1950	2	5	2	3		2	5	3	4	
	Type III—Low Density, No Perennial Grass					Type IV—Low Density, *Poa caespitosa* Present				
	Defoliation Treatment				Significance of Treatment Differences	Defoliation Treatment				Significance of Treatment Differences
	1	2	3	4		1	2	3	4	
No. crowns per sq. lk. 26.iv.1949	1·16	1·08	1·16	1·28		1·48	1·40	1·52	1·48	
Proportion present 14.xi.1949	0·18	1·09	0·83	2·01	$P<0\cdot001$	0·11	0·33	0·82	1·13	$P<0\cdot001$
Proportion present 10.ii.1950	0·03	0·20	0·05	0·25	Not significant	0·02	0·08	0·00	0·08	Not significant
No. of plots occupied 10.ii.1950	1	2	1	4		1	2	0	2	

* Treatment 1. Defoliated from 26.iv.1949 to 14.xi.1949.
Treatment 2. Defoliated from 22.viii.1949 to 14.xi.1949.
Treatment 3. Defoliated from 22.viii.1949 to 9.xii.1949.
Treatment 4. Defoliated from 7.x.1949 to 9.xii.1949.

weed's root system, the plant soon achieves its former predominance. When distribution is taken into account, it may be concluded that treatments 1 and 3 resulted in highly effective destruction in all four types of stand. Treatment 2 was not severe enough to prevent recovery in high-density stands, but was highly effective in low-density wort, with or without perennial grass. Treatment 4 was also efficient in low-density wort, and in high-density wort where *Poa* was present.

The results indicate that *Hypericum* is particularly susceptible to defoliation in the late spring when growth is most rapid (see Clark and Clark 1952, Fig. 1). However, defoliation by adult beetles is, in practice, neither as severe nor as sustained as in treatments 3 and 4. Complete defoliation by adult beetles over extensive areas has only been observed where the insects form a "feeding front" (Clark and Clark 1952; Clark 1953), and gradually eat their way through stands of weed surrounding the sites defoliated by larvae. Only the weed attacked by the first emerging adults is completely defoliated early in October, but by the middle of November this is well behind the "feeding front" and has been deserted by the beetles. Thus desertion of the areas in which the food supply is temporarily exhausted limits the period of defoliation when the plant is most susceptible.

The experiment supports Clark's (1953) conclusion that *C. gemellata* is a more effective destroyer of *Hypericum* than *C. hyperici* because it is able to cause complete defoliation early in the winter. Hand defoliation for a period resembling that caused by *C. hyperici* produced essentially similar results to those actually observed for the insect in the Ovens and Mannus Valleys. In both areas this insect has been really affective only in stands of *Hypericum* characterized by large plants at relatively low density. Finally, the apparent contribution of *Poa* suggests that the destructive effect of the insects may be increased by the presence of perennial grasses when competition for moisture is severe.

Further information on susceptibility to defoliation was obtained in 1949 by stripping plants by hand in a eucalypt forest and in a plantation area where the pines had been felled 3 years previously. In the first trial two plots, each 100 sq. lk. in area, were selected in wort stands typical of forest areas—one with *Poa* in abundance, and the other lacking perennial grasses. After the initial defoliation on May 2, 1949, the *Hypericum* was stripped of leaves and soft shoots at intervals of 2-3 weeks until December 12. In plot 1, containing *Poa*, the original density of 6.57 crowns per sq. lk. was reduced to 3.91 per sq. lk. by February 10, 1950. In plot 2, virtually a pure stand of the weed, the reduction was from 7.51 crowns per sq. lk. to 3.83 per sq. lk. In both plots the survivors were distributed throughout. The results indicate a very high degree of resistance to defoliation in such stands. Further, they suggest that neither chrysomelid would be effective in forest habitats even if they were able to multiply sufficiently to cause such defoliation. As Clark (1953) has shown, forest habitats are relatively unfavourable to both species in the Ovens Valley, and complete defoliation of the plant occurs infrequently.

The object of the second trial was to ascertain if susceptibility was related to the vigour of the plant as expressed by yield. In the experiments already

TABLE 5

REGENERATION OF ST. JOHN'S WORT IN VARIOUS HABITATS AT BRIGHT FOLLOWING PARTIAL OR COMPLETE DESTRUCTION OF THE ORIGINAL STANDS BY THE CHRYSOMELIDS

Habitat	Plot No.	Original Stand Destroyed	Density and Percentage Frequency of *Hypericum*						Dominant Species	Notes on Cover at Soil Surface and Grazing
			Crowns/ Sq. Lk.		Seedlings/ Sq. Lk.		Frequency of Crowns (%)			
			1949	1950	1949	1950	1949	1950		
Arable land, clay loam soil	A^1 (*a*)	1946	0·10	0·19	0·00	0·02	9	13	*T. subterraneum* and *Hypochoeris radicata*	Very dense low cover. Lightly grazed by rabbits only
Arable land, clay loam soil	A^1 (*b*)	1948	0·00	0·00	0·00	0·00	0	0	*T. subterraneum* and *Hypochoeris radicata*	Very dense low cover. Lightly grazed by rabbits only
Arable land, clay loam soil	A^2 (*a*)	1946	0·00	0·01	0·00	0·01	0	1	*Vulpia bromoides*	Very dense cover of litter from the previous season's growth
Arable land, clay loam soil	A^2 (*b*)	1948	0·02	0·06	0·00	0·00	2	6	*Vulpia bromoides*	Very dense cover of litter from the previous season's growth
Arable land, deep sandy soil	B^1 (*a*)	1946	0·00	1·17	3·00	0·57	0	55	*Vulpia bromoides*	Very sparse cover of annuals, no litter. Grazed by rabbits only
Arable land, deep sandy soil	B^1 (*b*)	1948	0·07	0·03	0·07	0·02	7	3	—	Dense litter of old wort stems, etc.
Arable land, deep sandy soil	B^2	1948	0·00	0·00	0·00	0·00	0	0	*Hemarthria uncinata*	Very dense cover. No grazing
Dredgings	C^1 (*a*)	1946	0·03	1·66	0·83	1·15	3	44	*Eragrostis* sp., annual grasses and herbs	Very sparse to dense cover in patches. Grazed by rabbits only
Dredgings	C^1 (*b*)	1948	0·01	1·52	3·83	6·56	1	62	*Vulpia bromoides*	Very sparse. Grazed by rabbits only
Native perennial grass pasture, clay loam soil	D^1	1946	0·32	0·51	0·08	0·33	21	30	*Themeda australis*	Cover very dense to sparse in small patches. Grazed by beef cattle from late autumn to spring, and by rabbits

TABLE 5 (*Continued*)

Habitat	Plot No.	Original Stand Des-troyed	Density and Percentage Frequency of *Hypericum*						Dominant Species	Notes on Cover at Soil Surface and Grazing
			Crowns/ Sq. Lk.		Seedlings/ Sq. Lk.		Frequency of Crowns (%)			
			1949	1950	1949	1950	1949	1950		
Native perennial grass pasture, clay loam soil	D^2	1946	0·20	0·53	0·13	0·00	14	32	*Poa caespitosa* and *Danthonia* sp.	Moderate cover. Grazed by beef cattle from late autumn to spring, and by rabbits
Native perennial grass pasture, clay loam soil	D^3	1946	0·24	0·58	0·14	0·00	18	39	*Poa caespitosa* and *Microlaena stipoides*	Dense cover, grazing as for D^1, D^2
Native perennial grass pasture, clay loam soil	D^4	1948	1·29	0·17	0·00	0·00	50	17	*Danthonia penicillata*	Very dense cover of grass tussocks, *Hypochoeris*, and *Trifolium* spp. Continuously grazed by sheep during 1949-50
Clearings in timbered areas	F^1	1946	0·90	1·21	1·40	0·00	47	64	*Poa*, *Danthonia*, and *Vulpia*	Moderate ground cover. Kept very short by heavy rabbit grazing
Clearings in timbered areas	F^2	1946	0·14	1·55	5·20	0·33	4	53	*Vulpia bromoides*	Sparse cover. Lightly grazed by rabbits only
Clearings in timbered areas	F^3 (*a*)	1946	0·12	2·01	1·96	0·44	8	47	*Vulpia bromoides*	Sparse cover. Lightly grazed by rabbits only
Clearings in timbered areas	F^3 (*b*)	1948	0·00	1·54	4·90	0·87	0	51	*Vulpia bromoides*	Sparse cover. Lightly grazed by rabbits only

reported, where yield per unit area was measured, there was either no correlation between yield and susceptibility (as in the hand defoliation experiment), or the lowest-yielding stands occurred on sites that produced the more resistant stands, e.g. eucalypt forest. It was possible in this case to select well-spaced plants, without suckers, all of which had flowered for the first time in 1948 and were approximately equal in age. Two lots of 10 plants were chosen on the basis of similar yield in 1948 (estimated in terms of the number and size of flowering stems). The mean number of flowering stems per plant in 1948 was 12.2 (range 10-18) in lot 1, and 4.4 (range 3-5) in lot 2. On June 7, 1949, the crowns were stripped of all but the main stems of the procumbent growth, and defoliation was continued at intervals of 2-3 weeks until no further regrowth was made. On December 8 only one plant in each group remained alive (represented by a sucker from the main root-stock). At no time was there any difference in the number of plants killed in each lot. The mean yield of shoots and leaves on June 7 was 9.2 g. per plant for lot 1, and 4.6 g. per plant for lot 2 (air-dry weight). There was no correlation between survival and the number of flowering stems in 1948, yield on June 7, or total yield in 1949. Thus susceptibility to defoliation was not related to vigour as measured. It depends apparently on the environmental factors that determine the tendency of the plant to reproduce vegetatively and the life span of the individual crown. The greater the predetermined tendency to sucker the greater is the resistance of a stand to defoliation.

IV. The Regeneration of Hypericum from Seed

(*a*) *Effect of Cover on Seedling Establishment*

The regeneration of *Hypericum* from seed, following destruction of the original stand by the insects, was studied in the permanent transects (see Section III(*a*)) and in small plots (0.25 sq. ch. to 2.0 ac.) distributed throughout the district. The latter included all the principal types of habitat except pine plantations and eucalypt forest. Regeneration in pine plantations was controlled by the density of the tree canopy. No stands have been destroyed in eucalypt forest.

Observations were made each year during the spring, when seedlings from the autumn germination were fairly well developed, and towards the end of the summer when seedlings from the spring germination had either died or become established. The plots were sampled by taking 100-300 random 1 by 1 lk. quadrats, the number depending on size and uniformity. In each quadrat the numbers of *Hypericum* crowns and seedlings were counted, and the presence of other plant species recorded. A seedling was recorded as a crown when it was well established, i.e. when approximately 9 months old.

In the sampling areas the original growth of *Hypericum* had been almost completely destroyed by insect attacks in 1946 or 1948, except in the plots containing perennial grasses, where a proportion of the original plants survived. Early in 1949 all other plots were almost completely free of the weed. The factors suppressing regeneration in 1947 are not known. The chrysomelids may have destroyed the seedlings in some sites. In 1948 the sampling areas were not invaded by the insects, and the failure of the weed to re-establish itself was due to unfavourably dry conditions for germination and seedling establishment (see next section).

The density and percentage frequency of *Hypericum* in September 1949 and 1950 are given in Table 5 for study plots that were not re-invaded by the insects in either year (all but five). The differences in the amount of regeneration were obviously related to the density of cover immediately above the ground surface, which in turn depended on soil conditions and the grazing factor. No seedlings were established where the ground surface received no direct illumination. In plots containing a fair cover of perennial grasses (D^1, D^2, D^3, D^4), subterranean clover, and *Hypochoeris radicata* (A^1), litter from the previous season's growth of *Vulpia bromoides* (A^2), or a dense cover of fallen wort stems (B^1 (*b*)), the few seedlings recorded were all found where the soil had been exposed by stock or rabbits, or by burning. For example, plot D^1 was burnt in the late summer of 1949-50. In plots B^1 (*a*), C^1, F^2, and F^3, little cover was provided by perennial species, practically no litter accumulated, and regeneration was limited only by soil moisture and temperature. Plot F^1 was located near a series of rabbit warrens and, although perennial grasses were present in all quadrats (as in all *D* plots), they were kept grazed almost to ground level and many wort seedlings survived.

By the end of 1950 approximately 50 per cent. of the quadrats in plots deficient in ground cover were occupied by flowering wort, and a further 25-40 per cent. were occupied by well-established seedlings. In the autumn of 1951 few seedlings were established, but much vegetative reproduction occurred. At the time of writing (June 1951) it seems practically certain that the weed will achieve its former abundance and productivity in most, if not all, of these plots either before re-invasion by the insects, or before they multiply sufficiently to cause much mortality. In several areas not included in this study the weed has already recovered completely.

Further observations on the effect of cover on seedling establishment were made in the grounds of the Field Station at Bright. Small plots were sown with *Hypericum* in the early autumn and watered when necessary to ensure favourable conditions for germination and seedling growth. The seeds of other plants present also germinated. This volunteer growth was allowed to developed unchecked in some plots and was removed in others. In consequence, the wort seedlings were subjected to various degrees of shading. Observations on survival were made during the winter and spring. Of the wort seedlings that grew in plots cleared of other growth, those bearing six leaves or less were killed by frost. The remainder succeeded in establishing themselves. In plots containing a sparse cover of erect annuals, mainly *Vulpia bromoides*, both small and large seedlings survived. The annuals apparently provided protection from frost. Where rosette-forming plants (*Hypochoeris radicata* and *Plantago lanceolata* L.) or species with a procumbent growth habit (*Trifolium subterraneum* and *Medicago denticulata* Willd.) were abundant, the wort seedlings died almost immediately after germination. The very high mortality must have been due to shading as moisture conditions were favourable.

Because of the high mortality resulting from inadequate illumination immediately after germination, little evidence is available on the effects of competing species on the seedling of *Hypericum* in its later stages of development. However, it has been observed that seedlings surviving the winter frequently disappeared during the spring in areas in which the associated flora produced a dense, tall cover. The plant probably remains sensitive to competition for light until it has accumulated reserves of carbohydrate that would enable it to withstand temporary shading. Once it has survived the critical period of establishment, *Hypericum* usually has an advantage over the associated grasses and herbs in competition for moisture and nutrients, owing to its ability to develop a more extensive root system and its capacity for vegetative reproduction. The increase in the density and abundance of *Hypericum* in the native perennial grass pastures (plots D^1, D^2, and D^3) and in plots A^1 and A^2 was due almost entirely to suckering. Thus the vast majority of the plants that provided sufficient cover to suppress the regeneration of *Hypericum* from seed were unable to prevent the spread of the weed by suckering.*

(*b*) *Effect of Temperature and Rainfall on Germination and Seedling Survival*

The germination and seedling establishment of *Hypericum* were obviously affected by temperature and rainfall. In 1948 germination was observed only during the late spring (November) in relatively moist sites. The weather was hot and dry during the following 8 weeks and practically all seedlings died.

Unfortunately, no detailed temperature records were available until 1949, when a standard screen was set up at the Bright Field Station. Table 6 summarizes the relevant temperature and moisture data in relation to germination observed in the field in 1949 and 1950. Most germination took place during the six warmest months. None occurred from May to August in either year, or in April and September 1949. In 1950 there was extensive germination very early in April, and limited germination in September. Table 6 suggests that germination is possible in the Bright area only when the mean screen temperature exceeds 51°F. A detailed examination of the field records in relation to temperature showed that the coolest germination period (September 1-15, 1950) had a mean screen temperature of 52.6°F., the mean daily maximum being 65.6°F. and the mean daily minimum 39.5°F. Under these conditions germination occurred only in sites that received the maximum amount of solar radiation during the day. During the warmest months extensive germination occurred when the Meyer ratio was 20 or higher for the period beginning with the first substantial fall of rain.

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* The application of common salt (e.g. by the Victorian Lands Department) to control the weed along roadsides and stock routes is an expensive process and has to be repeated year after year, as the weed soon reappears, not generally from seed, as is frequently supposed, but from young suckers missed during the salting. Control of rabbits would be a more effective method of preventing the spread of the weed into adjoining districts. These animals carry the seed and, by exposing the soil and reducing the surface cover, provide favourable conditions for seedling establishment.

Examination of the available rainfall records indicated that, in general, seedlings germinating early in March have the best chance of survival. At this time of year the temperatures are high enough for rapid growth and the subsequent autumn rainfall is comparatively reliable. It was observed that such seedlings were sometimes able to escape shading by winter-growing annuals. Although moisture conditions were equally favourable later in the autumn or early in the spring the growth rate was slower, and competitors, when present, had reached a greater size. Consequently, destruction by shading was more likely. The frequent occurrence of drought periods of 1-2 months during the late spring and summer invariably caused a very high mortality in seedlings germinating at this time of year.

TABLE 6

EFFECT OF SEASONAL CONDITIONS ON THE GERMINATION OF *HYPERICUM* IN THE FIELD (BASED ON STANDARD WEATHER RECORDS)

	1949				1950			
Month	Total Rain (points)	Meyer Ratio	Mean Temp. (°F.)	Notes on Germination	Total Rain (points)	Meyer Ratio	Mean Temp. (°F.)	Germination
Jan.	159	—	—	Nil	89	5	66	Nil
Feb.	151	5	67	Nil	399†	20	67	Extensive
Mar.	590	39	63	Extensive	616	34	65	Extensive late March to early April
Apr.	167	33	51	Nil	74	8	56	
May-Aug.	253*	110*	44*	Nil	253*	53*	47*	Nil
Sept.	440	88	49	Nil	466	52	53	Limited to warmer sites
Oct.	801	160	56	Extensive	605	55	57	Extensive
Nov.	536	88	62	Extensive	433	27	62	Extensive
Dec.	50	3	63	Nil	276	11	68	Limited to moister sites

* Means for months concerned.

† 377 Points in 8 days.

On the poorer soils, e.g. dredgings and sandy river flats, which support only a very sparse growth of other herbaceous plants, weather conditions had an important effect on the rate of regeneration of *Hypericum* from seed, after destruction of the original stand by the chrysomelids. For reasons discussed later, some *Hypericum* seeds do not germinate for years. However, varying percentages germinate whenever weather conditions are favourable and crop after crop of seedlings appears. If the early batches are destroyed by drought the beetle population is, of course, eliminated, and the weed has a chance to recover from later germinations before the insects return.

In 1946 the insects were responsible for very extensive destruction of *Hypericum* in many such areas, where they were present in millions. After final defoliation of the plants the adult beetles either migrated or died. Some sites remained free of the insects for 4 years, 1947-50. The gradual recolonization of one such area by *Hypericum* is shown by the following observations made along a permanent strip transect (400 by 1 lk.). Only one seedling was established in 1948. The following year, 56 March seedlings and 175 November seedlings survived. In 1950, 21 February seedlings became established. By the end of the year there were 253 well-established plants on the transect. These were the only survivors from populations of over 40,000 seedlings. Even if the site remains free of the beetles the weed will not achieve its former productivity before the end of 1952, i.e. approximately 6 years after the destruction of the original stand.

(*c*) *Inhibition of Germination*

The chances of successful regeneration from seed are increased by very high seed production per plant and by the apparent dormancy of a proportion of the seed. Ewart (1910), who found that "12 year old seed failed entirely to germinate," estimated the period for which seeds are able to lie dormant in the soil at 8-10 years. Present observations have shown that some seeds remain viable in the soil for at least 6 years.

A probable explanation of the apparent dormancy of some *Hypericum* seed was given by germination tests made in the laboratory. These tests followed field observations, which suggested the presence of germination inhibitors. In 1949 no seedlings were found in areas bearing well-established stands of *Hypericum,* and very few in places in which the original stands had been destroyed by the insects in 1948. However, seedlings were plentiful in areas where the original stands had been destroyed in 1946, although other species were frequently more abundant. In areas containing unattacked or recently destroyed stands the surface litter etc. was not always sufficiently dense to account for the absence of seedlings, and moisture conditions appeared to be quite favourable for germination. It seemed possible, however, that, if the oil in the leaves or the exudate of the seed capsules contained a germination inhibitor, the accumulation of decayed leaves and flower heads of *Hypericum* in the surface soil could account for the failure of germination.

A number of germination tests were carried out, either at fluctuating room temperatures or at a constant temperature of 68°F. (20°C.). Untreated seeds were compared with seeds moistened with various concentrations of aqueous extracts from macerated stems, roots, leaves, and seed capsules of *Hypericum.* The seeds were germinated in Petri dishes on filter paper moistened by water or by the various extracts. Each treatment was applied to four replicates of 100 seeds collected 9-12 months previously. All extracts from stems and roots, and the weaker solutions of leaf extract, had no effect on germination. Stronger solutions of leaf extract either reduced or inhibited germination. No seeds germinated in the presence of seed capsules or their extract.

In these tests germination of the untreated seeds was erratic and much lower than expected, the maximum percentage germination obtained being only 25 per cent. Examination of seeds that failed to germinate indicated that most were viable (germination continued over a period of months when the dishes were kept moist). On a variable proportion of these seeds the exudate of the seed capsule was visible as a small pellet adhering to the seed coat. If this substance acted as an inhibiting agent then the complete or partial failure of germination in the field could be explained by its presence both on the seed coat and in the litter of seed capsules in the soil. Before further laboratory tests were made, seedlings were found for the first time in a stand of *Hypericum* with the usual accumulation of litter at the soil surface. These seedlings appeared early in April 1950 after nearly 3 weeks of continuous heavy rain (616 points in 19 days). This suggested that any inhibiting substances present in the litter or on the seed were readily leached by repeated heavy rains, or sufficiently diluted to allow germination.

A further germination test was made, using seeds washed with several lots of rainwater over a period of 3 days. Washed seeds moistened with water only (i) were compared with:

(ii) Washed seeds moistened with concentrated leaf extract;

(iii) Washed seeds moistened with concentrated extract of seed capsules;

(iv) Unwashed seeds moistened with water only.

The treatments were first applied on November 16, 1950, after a few seeds in a preliminary test had germinated. However, germination soon ceased in this batch, and no germination occurred in any of the experimental treatments. Germination was apparently inhibited by high temperatures (daily maxima exceeding 80°F.). Consequently, the dishes were dried out and stored until March 22, 1951, when all treatments received water only. Germination began 6 days later. The percentage germinations and the associated temperature conditions are summarized in Table 7. Seven days after watering, the germination of washed seeds, moistened with water only, was much higher than for unwashed seeds or those treated with extracts. However, by the end of 14 and 28 days respectively, the percentage germinations in unwashed seeds and those treated with leaf extract had reached similar values. The germination of seeds treated with extract of seed capsules remained significantly lower than in the other treatments throughout the whole germination period (28 days).

The results suggest that there are substances present in the leaves and seed capsules that inhibit germination by reducing the permeability of the seed coat to water. The delay in germination of unwashed seeds could be due to the presence of a film of the seed capsule exudate which is gradually reduced or removed by water. Where this substance is more highly concentrated, as in treatment (iii), a relatively long period is required for water to penetrate the seed coat. The oil in the leaves, acting in a similar manner, was probably responsible for the delay in germination in treatment (ii).

It is not known whether the oil from the leaves is ever sufficiently concentrated in the soil to have any practical effect on germinations in the field. The effect of the seed capsule exudate is alone sufficient to explain much of the variation observed in field germinations and in laboratory tests.* Temperature and moisture conditions favouring germination in the field occur most frequently for short periods of 1-2 weeks, and rarely for as long as 4 weeks. Given favourable temperatures, the germination capacity of seed in the field would be affected by the amount and distribution of rainfall, movement of soil water, and the quantity of the exudate on the coats of seeds or in the soil matrix. It is suggested that the apparent dormancy of *Hypericum* seed is determined primarily by the sticky exudate of the seed capsule, which adheres to the seed coat and aids in seed dispersal; and secondarily by the immediate physical environment of the seed in the soil.

Table 7

PERCENTAGE GERMINATION OF ST. JOHN'S WORT

Means of three replicates of 100 seeds, 12 months old

Treatment	Germination After			Mean Maximum and Minimum Temperatures (°F.)
	7	14 (%)	28 Days	
(i) Washed seed	69	74	79	1st-7th day, 81·1-44·6
(ii) Washed seed+leaf extract	44	53	74	8th-14th day, 75·7-44·6
(iii) Washed seed+seed capsule extract	5	8	23	15th-28th day, 66·9-41·5
(iv) Unwashed seed	34	67	77	
Minimum difference for significance between treatment means	17	13	13 (5% level)	
	23	17	17 (1% level)	

V. Discussion and Conclusions

Previous observations (Clark and Clark 1952) and those described in the present paper have shown that *Hypericum perforatum* L. var. *angustifolium* DC possesses characteristics that make it a difficult species for effective entomological control. They include:

(i) The ability to prosper under a diversity of environmental conditions after successful establishment from seed;

(ii) A great capacity for vegetative reproduction; and

(iii) The delayed germination of a proportion of the seed. The problem of control is made more difficult in the principal infestation area by the limited distribution and abundance of herbaceous species capable of ousting mature plants after they have been damaged severely by insects (cf. the control of *Clidemia hirta* by *Liothrips urichi*, where such plants played an important role, according to Simmonds 1933). On the other hand, plants are already present in some parts of the area, or can be grown there, e.g. subterranean clover, which are able to prevent regeneration from seed.

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* It is possible that the results obtained by Cashmore (1939), indicating the need for a "resting period of four to six months," were due to the gradual drying and wearing away of the coating of exudate on freshly harvested seeds. The apparent stimulation of the rate of germination by the chemicals tested by him may have been due simply to the physical effect of washing.

In terms of the characteristics of the weed and the associated flora, the chance of effective entomological control would be greatest in treeless areas of comparatively deep soil, e.g. abandoned farmland and sandy river flats. Such areas are relatively favourable for the growth of other herbaceous plants, e.g. perennial grasses capable of competing effectively with damaged wort plants, and species like *Trifolium subterraneum* and *Hypochoeris radicata,* which can destroy seedling regeneration by shading. In the absence of perennial grasses, the deeper soils favour long crown life in *Hypericum* and limited suckering, i.e. produce the most susceptible growth forms of the mature plant. The chance of effective entomological control would be much less in treeless areas of shallow, stony soil. There, soil conditions favour almost continuous vegetative reproduction. As a result, the proportions of young, mature crowns are always relatively high and stands tend to be more resistant to insect attack. Characteristically, such areas are unfavourable for the growth of most other herbaceous plants, and species capable of competing effectively with any stage of *Hypericum* are usually scarce or absent. Insects are least likely to be effective in the areas of eucalypt forest on the hills adjoining the valleys. The tendency of the weed to sucker is greatest in such areas, and consequently the destruction of the stands is more difficult to achieve than elsewhere.

Broadly speaking, this order of effectiveness has been realized in the results shown by *C. gemellata* and *C. hyperici.* However, as demonstrated by Clark (1953), the characteristics of the insects have, in general, been primarily responsible for determining their relative effectiveness in the different types of habitat. Treeless areas of deep soil provided either the most favourable habitats for the survival and multiplication of both chrysomelids during the initial period of colonization,* or less favourable habits in which, however, perennial grasses such as *Themeda* were sometimes present to assist the beetles. In many treeless areas of shallow stony soil the insects were eliminated annually by mortality and migration—principally the former.† Both chrysomelids have shown a marked tendency to avoid entering timbered sites, which have thus been colonized less successfully than treeless areas.

It so happens that environmental conditions are most favourable for colonization by these insects in the very sites in which the weed is most readily controlled, and least favourable where the weed would be most difficult for them to destroy. The results of the present study suggest that even if the insects had been able to colonize, initially, all types of habitat equally well, the degree of control achieved would still have been influenced substantially by differences in the environmental conditions affecting the plant.

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* They included Clark's (1953) "dense wort" habitats, which were stands of large wort plants of dense growth habit.

† They included most of Clark's (1953) "sparse wort" habitats, which were stands of smaller wort plants of relatively sparse growth habit.

VI. ACKNOWLEDGMENTS

My thanks are due to Mr. L. R. Clark for many helpful discussions, and to Mr. E. E. Lewis and Mr. E. R. Pearce for technical assistance in the field.

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THE GENUS *TRIODIA* R.BR. (GRAMINEAE)

By NANCY T. BURBIDGE*

[*Manuscript received April* 30, 1952]

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Summary

The material of *Triodia* R.Br. available in Australia was used as a basis for a revisory study of the genus.

Relationships between the species and the affinities of the genus with *Plectrachne* Henr. and *Danthonia* DC. are discussed. The opinion is expressed that the genus is better placed in the tribe Danthonieae than in the Eragrosteae.

Consideration is given to the possible history of the genus in the light of recent papers on past climatic conditions in Australia.

A key is provided for the identification of 28 species and a number of varieties.

All species and varieties are fully described and most of them illustrated. The following new species are described for the first time: *Triodia marginata, T. plectrachnoides, T. burkensis, T. inutilis, T. molesta, T. scariosa, T. roscida,* and *T. spicata.* The following varieties are also new: *T. pungens* var. *linearis, T. mitchelli* var. *breviloba, T. mitchelli* var. *pubivagina, T. irritans* var. *compacta, T. irritans* var. *laxispicata.* In most cases, though not all, the varietal epithet has been used where the specimens do not seem to represent truly discontinuous populations so that specific ranking was not warranted.

Maps showing the distribution of the species and varieties have been included.

INTRODUCTION

In 1943 the author completed a taxonomic study of the species of *Triodia* R.Br. occurring in Western Australia (Burbidge 1946*a*). This was followed

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* Division of Plant Industry, C.S.I.R.O., Canberra, A.C.T.

by studies on the morphology and anatomy of the same species (Burbidge 1945*a*, 1946*b*, 1946*c*). Later a study of the whole range of herbarium material of the genus available in Australia was undertaken and this paper is the result.* During the period of the investigations specimens collected in the north by the members of the Northern Australian Regional Survey have filled in a number of gaps in the records and have also brought to light several new species. With these, as well as with the material from the various Australian herbaria, it has been possible to reach certain conclusions regarding the affinities between the various species and their possible origin, though unfortunately it has not yet been possible to test these ideas by means of cytological studies. Little seed of the species is available. Most herbarium specimens have few mature seeds in the spikelets and apparently the plants set very little in the field. Also, owing to the general inaccessibility of the areas in which most of the species grow, it has not been possible to obtain transplanted material.

The fact that the majority of the species occur in remote areas that have not yet been scientifically studied makes it possible that more species will be discovered in the future. Also, the relationships between some of the species will be clarified. However, with the exception of some of the eastern material the specimens fall readily into discrete groups. Where perplexing variations do occur, as in the groups allied to *T. mitchelli* Benth. and *T. irritans* R.Br., some of the material has been placed under varietal names. While the populations, as represented by the available material, to which these varietal names have been given display characteristic morphological differences allied to a geographical scattering, the discontinuity between them is not a clear one. Not only is there a blurring of morphological differences but there are differences in the degree of distinction of the respective varieties. In some cases these complex groups may represent forms that have not yet attained sufficient differentiation to warrant specific ranking but further information is required before a thorough analysis can be made. Consequently the arrangement used in this paper is regarded as an interim one pending closer study in the field and some cytological investigation of the various representatives.

ECONOMIC IMPORTANCE

Over the last decade increasing attention has been focused on the potentialities of the northern parts of Australia, including the arid portions in which species of *Triodia,* commonly referred to as "spinifex," form a characteristic feature in the vegetation. The fodder value of these coarse tussock grasses is limited by the palatability factor, and assessment of their importance to the pastoral industry should be based on the extent of the ecological associations in which they occur as well as the relative value of different species or the relative value as compared with other native grasses in the same localities.

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* Preparation of this paper was completed late in 1951. Since then the author has been able to consult the material at the Kew Herbarium. As a result the text has been modified in some places and certain other comments will be made the subject for a further communication at some future date.

In most areas the plants occur on the poorer soils, i.e. on sandy or light soils where available water is low or on skeletal soils such as those found on stony ridges or low hills. As a general observation they are replaced by more valuable grasses on heavier soils, especially alluvial ones subject to flooding. Climatically the species are associated with areas receiving summer rains even though these may be low in quantity or unreliable in incidence. The group of species around *T. irritans* form an exception to this in that they are found in southern Australia in areas where there is either a low winter rainfall or where the rainfall is not markedly seasonal and is always highly variable in intensity.

Very few of the species are eaten by stock, even under stress, and of those that are relatively palatable only those with a leaf of the type found in *T. pungens* R.Br. need be considered. All the remainder are avoided because of their rigidly divergent and pungent-pointed leaves, which make it almost impossible for a soft-nosed animal to graze on them. In some cases the panicles of these may be grazed but this does not represent any appreciable addition to the food supply, especially since at the time the panicles are most palatable the stock are grazing on ground herbage. It is only when the herbage is gone that they turn to the tussock grasses.

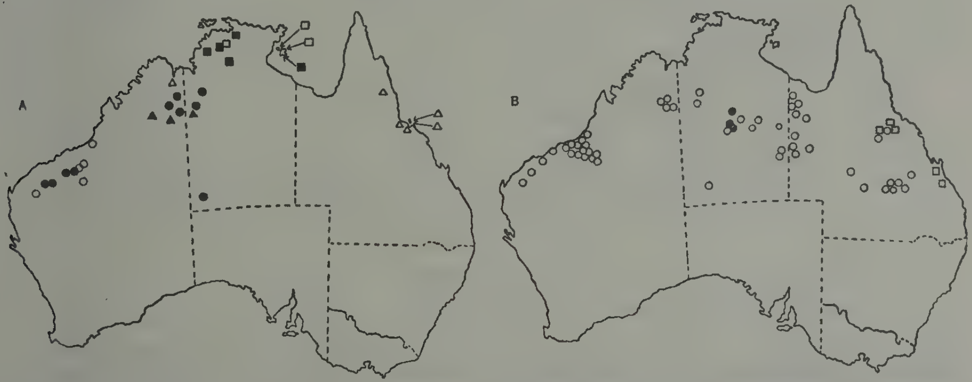

Fig. 1.—*A*, ● *Triodia wiseana*; ○ *T. wiseana* var. *brevifolia*; ▲ *T. intermedia*; □ *T. procera*; ■ *T. microstachya*; △ *T. stenostachya*. *B*, ○ *T. pungens*; □ *T. hostilis*; ● *T. pungens* var. *linearis*.

As will be seen from Figure 1*B*, *T. pungens* has a very wide distribution. In Central Australia and in Queensland it occurs in areas either practically unstocked or where better feed is available from other grasses except during drought. In Western Australia it presumably occurs in the Carnegie region between the Oakover River and the Northern Territory border but, as yet, no pastoral leases have been taken up in this inaccessible country. However, in the Pilbara region between the Hamersley Range and the De Grey River and in the coastal fringe extending north and up the Fitzroy River *T. pungens* is commonly a dominant species over considerable areas where it has a similar role to that of the chenopodiaceous shrubs of the southern arid pastoral country. The ecology of the spinifex country of the Pilbara has been discussed in earlier papers (Burbidge 1944, 1945*a*, 1946*a*), and similar areas in Queensland have been described by Blake (1938). Generally speaking, the maintenance of stock (usually sheep) on such areas depends on proper management which, while utilizing the herbage appearing after rain, retains the tussocks as a reserve without seriously affecting the natural regeneration. In many places burning is carried out to encourage a regrowth not only of young tussocks but also of the herbage (Burbidge 1944).

The other species having leaves similar to those of *T. pungens* (Figs. 1*A*, 2*A*) occur either in the extreme north or in eastern Australia. In either case they are not particularly important though the areas may be used for occasional grazing.

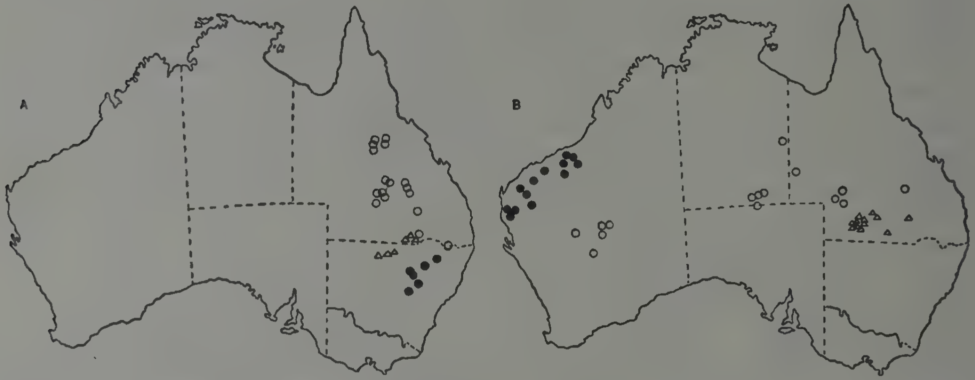

Fig. 2.—*A*, ○ *Triodia mitchelli* var. *mitchelli*; ● *T. mitchelli* var. *pubivagina*; △ *T. mitchelli* var. *breviloba*. *B*, ○ *T. basedowii*; ● *T. lanigera*; △ *T. marginata*.

DISTRIBUTION

A general idea of the spread of the various species can be obtained from Figures 1-4, which have been based on the material available during this study and on the specimens cited in the revision of the Western Australian species.

Much the most widely occurring species is *T. pungens*, which is found throughout the arid tropics from the west coast to eastern Queensland (Fig. 1*B*). As a broad generalization it can be pointed out that the distribution of the remaining species is, to some extent, peripheral to that of *T. pungens*. Where the areas of distribution overlap it is usually found that the species occupy different habitats. For example, *T. longiceps* J.M.Black is widely distributed across the southern part of the area for *T. pungens*, though it does not extend so far east, but occurs along small, dry watercourses and in rocky gullies rather than in the open habitats favoured by *T. pungens*.

Some species showing close affinities are confined to the same area. *T. secunda* N.T.Burbidge and *T. angusta* N.T.Burbidge in the Pilbara (Fig. 4*B*) and *T. roscida* sp. nov., *T. fitzgeraldii* N.T.Burbidge, *T. racemigera* C.A.Gardner, and *T. triticoides* C.A.Gardner in the Kimberleys (Fig 3*B*) all have the spikelets secund and more or less spicate on alternate lateral branches of the panicle. It is possible that future collections will close the gap between the areas where these species have been obtained. The complex around *T. mitchelli* is restricted to eastern Australia and is particularly associated with the western slopes of the Dividing Range. As has been mentioned in the previous section the group around *T. irritans* is restricted to the arid south and most of them occur in the mallee areas, the southern parts of the mulga country, or in isolated habitats on the western slopes of the Dividing Range in New South Wales.

DIAGNOSTIC CHARACTERS

Before proceeding to a discussion of the various species and of their relationships it seems advisable to describe the characters on which both discussion and separation of the various species have been based.

Vegetative.—All the plants show a characteristic form of culm development during which alternate series of long and short internodes are produced (Burbidge 1945*b*). Normally the stolons resulting from the long internodes are unbranched. The nodes of the tufts formed by the short internodes develop axillary shoots which may be short, or may develop into long stolons with an apical series of short internodes. The apex above the short series produces a terminal panicle and panicles may also develop from the ends of the short laterals. The plant as a whole is a coarse tussock with projecting, pungent-pointed leaves.

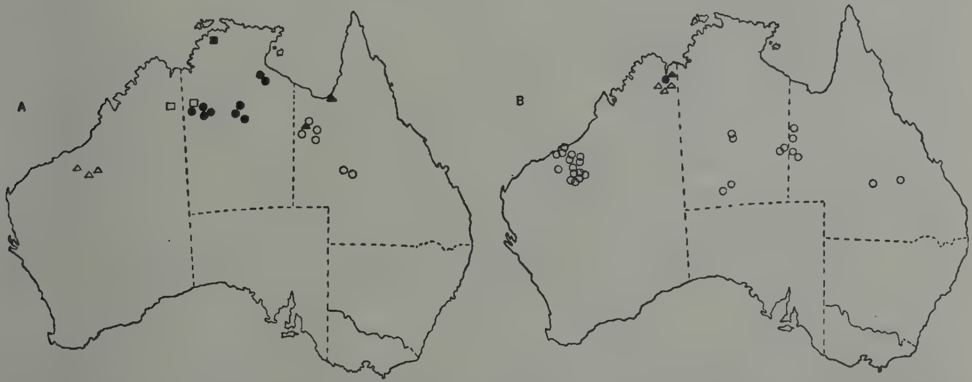

Fig. 3.—A, ○ *Triodia molesta;* ● *T. inutilis;* △ *T. brizoides;* ▲ *T. burkensis;* ☐ *T. roscida;* ■ *T. plectrachnoides.* B, ○ *T. longiceps;* ● *T. racemigera;* △ *T. triticoides;* ▲ *T. fitzgeraldii.*

The leaves are of particular importance since the structure of the lamina and the type of hairs produced at the orifice are both useful diagnostic features.

The laminae are of two main types. In one—typified by *T. pungens*—the abaxial surface is grooved on either side of the mid nerve and the subsidiary lateral nerves but not between the main lateral nerves (Burbidge 1946*b*). The result is that there is a smooth band along the lamina on either side of the median grooves. This character, which is clearly recognizable in herbarium specimens, is always associated with laminae having weakly pungent apices and with resiniferous sheaths. In the second type of laminae there are grooves between all nerves on the abaxial surface, the apices are rigidly pungent, and the sheaths lack resiniferous tissue.

Some of the differences in the hairs of the orifices in different species were described elsewhere (Burbidge 1945*b*) but a study of the figures accompanying this paper will show that they are sometimes sufficiently characteristic to permit identification even in the absence of panicles, particularly with species having the second type of lamina. The ligule is almost always a series of short cilia extending across the whole of the top of the sheath on its inner face and has no diagnostic value.

Reproductive.—The panicles are of four types, (*a*) an open structure of pedicellate spikelets loosely arranged on scattered or sparsely grouped lateral branches, (*b*) large panicles with very numerous irregularly arranged lateral branches bearing very small, numerous spikelets, (*c*) narrow panicles with the spikelets secund and either spicate or shortly racemose along alternate lateral branches of the main rhachis, and (*d*) sessile spikelets along the main rhachis (one species only).

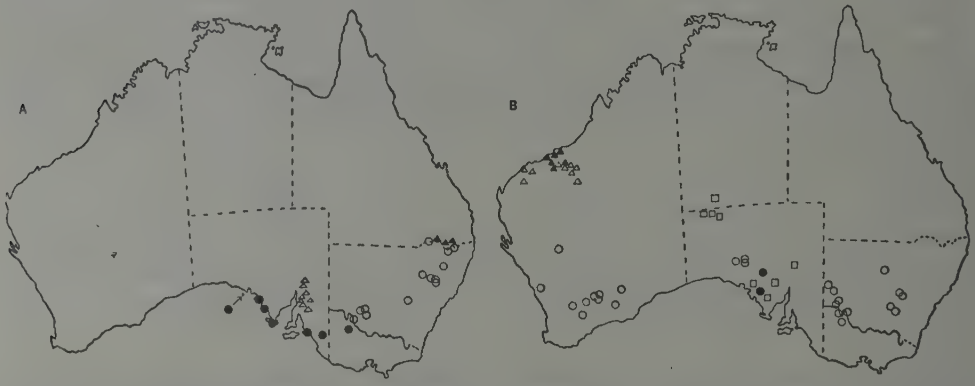

Fig. 4.—A, ● *Triodia irritans* var. *compacta*; ○ *T. irritans* var. *laxispicata* forma A; △ *T. irritans* var. *laxispicata* forma B; ▲ *T. irritans* var. *laxispicata* forma C. B, ○ *T. scariosa*; ● *T. lanata*; ☐ *T. irritans* var. *irritans*; △ *T. angusta*; ▲ *T. secunda*.

The chief characters in the spikelets are (*a*) the depth of the lobing of the lemmas, (*b*) the type and arrangement of the pubescence on the dorsal face of the entire portion of the lemmas, (*c*) the texture of the lemma, (*d*) the nervation of the lemma, and (*e*) whether the nerves of the palea are or are not alate.

INTERGENERIC RELATIONSHIPS

Intergenerically there is a close affinity with *Plectrachne* Henr. as has been previously discussed (Burbidge 1946*c*). The chief differences between the genera are the relatively longer glumes and the much deeper lobing of the lemmas in *Plectrachne.* The lobes of the lemmas in this genus are commonly referred to as awns and are always several times longer than the entire base. Apart from this, however, there is a remarkable degree of parallelism. Both the types of laminae found in *Triodia* are also developed in *Plectrachne* while vegetatively the plants are so similar that they may be confused in the field if panicles are absent. Similar types also occur in the panicles. *P. bynoei* is described as having spikelets imbricate on one side of the slender branches of the panicle, which suggests a similarity with such species as *T. fitzgeraldii* and *T. racemigera*. Finally there is parallelism in the structure of the lemma. The nerves are arranged in 3 groups of 3 each (rarely more) or the central one of each group may be developed with or without vestigial traces of the laterals. In *Plectrachne pungens* (R. Br.) C. E. Hubbard and *P. schinzii* Henr. the nerves are clearly visible as a group of 3 in each awn but they are obscure in the hardened entire base—a condition also found in *T. pungens* (which has a similar leaf anatomy), *T. basedowii* Pritzel, and *T. lanigera* Domin. The last-named species also has the paleas coriaceous in the lower part as in the above species of *Plectrachne*. Areas of distribution of these species of the 2 genera overlap to a considerable extent. On the other hand, in the southern representatives of the genera, *T. scariosa* sp. nov. (*T. irritans* of most Western Australian publications), *P. bromoides* (F. Muell.) C. E. Hubbard, and *P. danthonioides* (F. Muell.) C. E. Hubbard all have thin lemmas in which the central nerve of each triplet is well developed and passes into the lobes while the laterals are either very thin and do not pass into the lobes or are absent.

Apart from the marked relationship with *Plectrachne* the spikelets in *Triodia* show some resemblance to those in *Danthonia* DC. where the central lobe of the lemma is a twisted awn. It is interesting to find that in the lateral lobes of the lemmas in *Danthonia* there is a definite tendency for the nerves to be conspicuous and similar to those in *Triodia*. While the central lobe in *Danthonia* is usually 1-nerved the base may appear to be 3-nerved owing to the presence of an anastomosing nerve connecting with the inner nerve of the lateral group or with a nerve alongside it that does not extend into the lateral lobe. In *T. mitchelli* and its varieties there is a similar nerve between the lateral and central triplets, though in some cases it is not very conspicuous (Figs. 7, 8). In this case the extra nerve enters the middle lobe, which is therefore 5-nerved at the base. In *T. basedowii* and *T. lanigera*, where the lobes are commonly more than 3-nerved, it is possible that additional nerves are also developed between the main nerve triplets. However, in these species the nerves are quite obscure in the indurate base so that the arrangement is not evident. If the morphological relationship between *Danthonia* and *Triodia* is significant then it is possible that the development of these additional nerves, which are little more than vestigial in *Triodia*, may be a primitive feature in the latter genus.

Most authorities place *Triodia* in the Eragrosteae where by definition (Hubbard 1934) the lemmas are 3-nerved. In such genera as the American *Tridens* Roem. and Schult. and *Triplasis* Beauv., which were formerly included in *Triodia* and in which the lemmas are 3-nerved, this is reasonable. But in *Triodia* R. Br. sens. str. the lemmas are rarely 3-nerved and are only so where the laterals of the nerve triplets have not been developed, a condition seldom encountered. Consequently it seems more logical to place both *Triodia* and *Plectrachne* with *Sieglingia* (another genus formerly included under Brown's generic name) in the tribe Danthonieae as defined by Hubbard (1948), where the figures of the lemma in *Sieglingia* may be compared with the condition described above.

INTERSPECIFIC RELATIONSHIPS

In order to indicate resemblances the species can be arranged as follows but it should be stated that this grouping, which has been followed in the key to the species, does not necessarily show the relationships in a phylogenetic sense.

Group I. Leaves of the *T. pungens* type with resiniferous sheaths.

- *A.* Species with very large panicles 20-60 cm. long and small spikelets (*T. procera* (leaves not typical), *T. microstachya, T. stenostachya, T. cunninghamii* Benth.).
- *B.* Panicles rarely more than 30 cm. long, branches not very numerous, and spikelets more than 6 mm. long (*T. pungens, T. hostilis* Domin, *T. mitchelli* and its varieties, *T. marginata* sp. nov.).

Group II. Leaves with evenly striate laminae, sheaths non-resiniferous.

- *C.* Panicles open or narrow but the spikelets loosely and irregularly racemose along alternate lateral branches.
  - (i) Lemmas very deeply lobed, the lobes stiffly scarious above the horny-indurate base (*T. basedowii* and *T. lanigera*).
  - (ii) Lemmas never very deeply lobed, the lobes similar in texture to the base.
    - (*a*) Orifice with bright hairs up to 5 mm. long (*T. wiseana* C. A. Gardner, *T. intermedia* Cheel, and *T. plectrachnoides* sp. nov.).
    - (*b*) Orifice with woolly tomentose hairs (*T. brizoides* N. T. Burbidge, *T. burkensis* sp. nov., *T. inutilis* sp. nov., and *T. molesta* sp. nov.).
    - (*c*) Orifice with very short erect hairs or almost glabrous (*T. longiceps, T. irritans* and its variety, *T. aristata* J. M. Black, *T. scariosa,* and *T. lanata* J. M. Black).
- *D.* With spikelets conspicuously secund and more or less spicate along alternate lateral branches of a narrow panicle (*T. angusta, T. secunda, T. roscida, T. triticoides, T. fitzgeraldii,* and *T. racemigera*).

- *E.* Panicle a narrow spike with biseriate spikelets (*T. spicata* sp. nov.).

As was stated in the previous section a characteristic feature of the genus is the development of 3 nerve groups in the lemmas, each group usually of 3 nerves, though in *T. mitchelli* sens. lat. there is an additional nerve between the lateral and median triplets, in *T. basedowii* and *T. lanigera* there are extra laterals in each lobe while, on the other hand, in species where lobes are short the lateral nerves of each triplet may be vestigial (Fig. 14 *et seq.*). The writer is of the opinion that development of the genus has been accompanied by a reduction in the nerves, i.e. the more primitive representatives should be sought among the species in which the groups are most evident, e.g. *T. mitchelli* and *T. pungens* in the first group and *T. basedowii* in the second.

If, as has been suggested above, the presence of additional nerves between the lateral and central triplets represents a primitive character then *T. mitchelli* may have appeared before *T. pungens*. But on the other hand, *T. pungens* over its much wider range appears to be a more polymorphic species exhibiting a number of generalized features that suggest affinity with a greater number of species in both group I and group II than does *T. mitchelli*. For example, both the small spikelets in *T. pungens* var. *linearis* and, in some other specimens, panicles with comparatively long branches with racemose spikelets suggest an approach to the conditions in *T. stenostachya* and *T. microstachya*. Again the specimens of *T. pungens* from the Pilbara region in Western Australia have lemmas with horny, indurate bases showing an affinity with *T. basedowii* and *T. lanigera*.

The depth of lobing of the lemma varies to a certain extent in both *T. pungens* and in the varieties under *T. mitchelli* but it is not clear what relationship exists between either of these species and the short-lobed, fewer-nerved lemmas of the species in group II. The reduction of the lobing of the lemma reaches its limit in *T. spicata* where the apex is acuminate, not lobed. Owing to the lack of clearly defined affinities it seems probable that short-lobed lemmas with fewer nerves may have arisen at different times and from differing ancestral forms.

Discussion and Conclusions

T. basedowii and *T. lanigera*, while sharing the superficial character of the laminae characteristic of the species in group II, have 2 pairs of subsidiary nerves on either side of the mid nerve (Burbidge 1946*b*), a feature also seen in *T. pungens*.

The available information is not sufficient to form a basis for the postulation of a centre of origin for the genus. There is no evidence that it occurs outside Australia and a non-Australian origin appears most improbable on the grounds of the ecological habitats occupied today, the existence of sea barriers to the north at least since the Pleistocene (Edgeworth David 1950), the past climatic history of the continent, and the morphological affinities.

Crocker and Wood (1947) suggest, on geological and pedological grounds, that Australia was subjected to a major change in climate at the end of the Pleistocene and that there have been only minor climatic fluctuations during the intervening period. The Pleistocene pluvial cycle is believed to have had an abrupt conclusion with a consequent wholesale destruction of the pre-arid flora, which is now represented mainly by relic areas in the south-western, southern, and south-eastern portions of the continent or in refugia. However, considering that there have been no major changes in topography, the pluvial cycle would have been characterized by some zonation in rainfall comparable with that of the present. There must have been a central area with a relatively dry climate in which the chief representatives of the present arid flora of inland Australia, or at least their ancestral forms, would have existed. Among the constituents of such a restricted arid flora *Triodia* was probably, if not certainly, represented.

If the view that ancestral forms were present is accepted, in the absence of any evidence that *Triodia* spp. have ever been constituents of the flora in higher-rainfall areas, then spread and development would have been facilitated by the change to arid conditions and by the reduced competition following the destruction of the pre-arid flora. According to Crocker and Wood this destruction was followed by widespread erosion and loss of soil stability, resulting in the production of the main dune systems of the present day (Crocker and Wood 1947, Fig. 3). In this connection it is interesting to find that the distribution of a number of *Triodia* spp. is associated with, or peripheral to, that of the dune systems of Central Australia. Where the species occur outside these areas they are found on skeletal or light-textured soils, i.e. in ecological habitats similar to those which must have been most prevalent in Central Australia following the onset of aridity.

The author is of the opinion that the climate of the arid period was not much drier than that of the present day and bases this statement on the fact that there are species of both plants and birds restricted to the extreme south-western corner of Western Australia that would probably be eliminated if the climate became markedly drier. In both cases the affinities are with species elsewhere in Australia so that it is unlikely that they are of recent origin. In other words, the aridity is a matter of comparison with the previous pluvial conditions rather than with the climate of the present day. If the climate has not been much more arid then Central Australia has had a fairly constant climate over a long period since the minor fluctuations would cause movements of the surrounding rainfall belts rather than marked changes in the rainfall of an already desertic region in the interior. The greatest effects on the flora would have been felt in the intermediate zones between the relic areas of the south (and possibly the north) and the central area. Within the intermediate or marginal areas one would expect also to find an admixture of forms from both main floristic types with a consequential increase in the degree of variation resulting from the greater amount of gene material available. Under these conditions the effects of the climatic fluctuations would be to favour the perpetuation of newly arisen forms and such marginal areas should be characterized by a richness in variability in both populations and in species. What is probably one such marginal zone is found between the highly endemic flora of the south-western corner of Western Australia, i.e. the South West Province of Gardner (1942) and that of the Eremaea, while others probably occur to the west of the Dividing Range in eastern Australia and in parts of northern Australia, though in the first of these latter the picture is complicated by the variable topography and soil pattern and in the second the data are too inadequate to permit speculation.

One of the chief characteristics of the flora of inland Australia is the large number of species that occur throughout the entire range with comparatively little indication of the development of geographic races from either west to east or north to south, i.e. there is in general a great uniformity. This is not to be taken as meaning that there is little variation in form but that the variations that do occur tend to be repeated through the range of distribution, e.g. variations in the *Dodonaea viscosa* L.-*D. attenuata* A. Cunn. complex, in *Eremophila latrobei* F. Muell., and in the mulga (*Acacia aneura* F. Muell.), many of which are repeated, so far as the outward morphology indicates, throughout their respective ranges.

The distribution of *Triodia*, as given above, exhibits two main features. Firstly there are several widespread species ranging through much of Central Australia and including representatives of both the main morphological and anatomical types, and secondly there are a number of others grouped around the periphery, especially around the area covered by *T. pungens* (Figs. 1-4). This is to say that the number of species is greatest around the periphery of the generic range and is in agreement with the hypothesis that speciation has been most marked in the areas subjected to climatic fluctuations during post-Pleistocene times. It is consistent with such a view that species with marked affinities such as those of the *T. roscida-T. fitzgeraldii-T. ramigera-T. triticoides* group, such species as *T. secunda* and *T. angusta*, or the forms in the *T. mitchelli* complex or the *T. irritans* complex are restricted to portions of the periphery and that there would appear to have been some interaction between *T. pungens* and *T. basedowii* in the De Grey River area of Western Australia (even though there is an absence of any similar relationship between them in Central Australia) and between *T. pungens* and *T. mitchelli* in the parts of Queensland for which *T. hostilis* has been recorded. From the information available it appears possible that *Triodia* was present in the flora of the interior before the onset of arid conditions, that it then spread over a wide area, and that the relatively constant climate of Central Australia during the post-Pleistocene has resulted in a wide distribution of a few species while minor climatic fluctuations have produced, in the marginal zones, conditions favourable for the differentiation and perpetuation of a number of species restricted in range, or, in *T. mitchelli* sens. lat., *T. irritans* sens. lat., and the De Grey forms of *T. pungens* (Burbidge 1946*a*), of forms that do not seem to be sufficiently distinct morphologically to justify specific ranking.

If the inferences drawn above are correct then similar distribution patterns should be discernible in other Australian genera. While the available data are not conclusive they include details that are in agreement. In the closely related genus, *Plectrachne*, for example, it may be significant that *P. schinzii* and *P. pungens*, in which the leaf anatomy is closely similar to that of *T. pungens* (Burbidge 1946*c*), are widely distributed in the arid parts of northern Australia while species with more specialized leaf anatomy are, like their anatomical counterparts in *Triodia*, restricted to the marginal areas, e.g. *P. danthonioides*, *P. bromoides*, and *P. dielsii* in the southern Eremaea of Western Australia.

The distribution maps published with the revision of *Swainsona* by Lee (1948) show that there is a zone in which the number of species, and of subspecies, is high along the western slopes of the Dividing Range in New South Wales and northern Victoria (cf. the *galegifolia* group, the subspecies of *S. greyana* Lindl. and *S. oroboides* F. Muell. ex Benth., the *swainsonoides* group, the *monticola* group, and the subspecies of *S. microphylla* A. Gray). *S. viridis* J. M. Black, *S. tephrotricha* F. Muell., *S. fissimontana* J. M. Black, and *S. stipularis* F. Muell. are associated with the refugium of the Flinders Range while the *macullochiana* group is centred in the Hamersley Range in Western Australia.

The latter area may be refugial in nature or a centre of speciation as it is high in endemics. In the interior, on the other hand, S. *rigida* (Benth.) J. M. Black, S. *phacoides* Benth., S. *oligophylla* F. Muell. ex Benth., S. *oroboides* (in part), S. *campylantha* F. Muell., and the members of the *canescens* group are all widespread.

Similarly in *Enneapogon* (Burbidge 1941) there are a few widely distributed species such as *E. polyphyllus* (Domin) N. T. Burbidge, *E. avenaceus* Lindl., *E. lindleyanus* (Domin) C. E. Hubbard, and *E. oblongus* N. T. Burbidge. The range of *E. nigricans* (R. Br.) Beauv. resembles that of the *Triodia irritans* complex as does, in a narrower sense, that of *E. cylindricus* N. T. Burbidge. *E. gracilis* (R. Br.) Beauv., *E. robustissima* (Domin) N. T. Burbidge, *E. pubescens* (Domin) N. T. Burbidge, and *E. asperatus* C. E. Hubbard are, with others, restricted to certain parts of Queensland and northern New South Wales. *E. pallidus* (R. Br.) Beauv., *E. purpurescens* (R. Br.) Beauv., *E. glaber* N. T. Burbidge, and *E. planifolius* N. T. Burbidge are northern while *E. clelandii* N. T. Burbidge appears to be restricted to the ranges of Central Australia, which appear from Crocker and Wood's comments to be refugial in nature.

In both *Eucalyptus* and *Acacia* (especially Section Juliflorae) there are indications of similar distribution patterns even though neither of them can be regarded as characteristic of the arid flora. In other groups the position is less clear since it becomes necessary to make a greater allowance for their ecological requirements. In the Andropogoneae, for example, the main genera are tropical rather than arid and hence it may be argued that distribution has been restricted by climatic zonation rather than that speciation has been related to zones of climatic fluctuation. However, in *Chrysopogon* there is, according to Blake (1944), the widely distributed *C. fallax* S. T. Blake with *C. pallidus* (R. Br.) Trinn. ex Stead., *C. sylvaticus* C. E. Hubbard, *C. latifolius* S. T. Blake, and others around the northern periphery. In *Bothriochloa, Capillipedium,* and *Vetiveria* distribution is more clearly related to the climatic zones of eastern Queensland and New South Wales but in *Dichanthium* the situation is rather similar to that of *Chrysopogon.*

In *Brachycome,* a genus that has probably spread from the relic areas of the pre-arid flora, the distribution as described by Davis (1948) is not easy to assess but it would appear that there are a considerable number of species along the drier slopes of the Dividing Range in eastern Australia. It is therefore possible that here also it may be possible to show a correlation between species pattern and past climatic variations.

Thus the conclusion reached from a consideration of the distribution of the species of *Triodia* and of other genera is that, at least in some genera, and in certain zones, speciation has been most pronounced around the circumferences of the generic ranges. The variations in climate during the post-Pleistocene appear to have been a major influence in the development of the present Australian flora. In a broad sense variation and the differentiation of species will be found to be highest in zones where the effects of climatic fluctuations have been most marked though, of course, the position of the zones of variability will vary slightly for different genera in accordance with both their ecological requirements and their relationships with the main floristic regions. With such a circumferential differentiation of species there can be little profit in attempting the preparation of diagrams or in mere speculation as to relationships between the whole group of species within a genus such as *Triodia.*

Citation of Species

In all cases the specimens listed under the species descriptions have been seen by the author. For Western Australian material reference is also made to the specimens listed in the revision of the species occurring in that State (Burbidge 1946*a*) but the material is not re-cited. The locality records provided by these latter specimens were, however, utilized during the preparation of the distribution maps (Figs. 1-4).

Where several specimens from one herbarium are listed the name of the appropriate Herbarium is given at the end of a consecutive series. The specimens are also listed so that the localities are arranged geographically from north to south and from west to east of the area of distribution. The locality of the specimens is indicated according to the following code.

AD	Herbarium of the Department of Botany, University of Adelaide, S.A. (includes Tate Herbarium).
ADW	Herbarium of the Waite Agricultural Research Institute, Adelaide.
BRI	Botanic Museum and Herbarium, Brisbane, Queensland.
CANB	Herbarium of the Division of Plant Industry, Commonwealth Scientific and Industrial Research Organization, Canberra, A.C.T.
MEL	National Herbarium of Victoria, Melbourne.
NSW	National Herbarium of New South Wales, Sydney.
PERTH	State Herbarium of Western Australia, Perth.

Genus TRIODIA Robert Brown

Triodia R.Br. in Prodromus Florae Novae Hollandiae 182 (1810).

Of Brown's 6 original species, *T. pungens, T. procera, T. microstachya,* and *T. irritans* are retained. *T. parviflora* was transferred to *Diplachne* and *T. ambigua* was listed as a synonym of *Diplachne fusca* by Bentham (1878).

The representatives are all perennial tussock grasses. The plants may be hemispherical, pyramidal, annular due to the death of the older, central culms, or may consist of a flat tangle of stoloniferous culms (Burbidge 1946*a*). *Panicle* an open structure of pedicellate spikelets or the spikelets racemose or spicate along lateral branches or, in one species, spicate along the main rhachis. In dried material the branches are commonly erect and may be loosely adpressed to the main rhachis. *Spikelets* linear to ovate, 3-20-flowered, the upper lemmas being male or sterile. Apparently little seed is set. Rhachilla usually fracturing below the floret so that the joint remains attached and lying against the back of the palea. *Glumes* subequal, 1-13-nerved but except in *T. basedowii* and *T. lanigera* rarely more than 7, of which the central one is usually better developed and sometimes sufficiently prominent to form a keel. *Lemmas* more or less 3-lobed, the lobes varying from longer than the entire base to mere indentations of the apex, each lobe with 3 nerves (except in *T. basedowii*, *T. lanigera*, and *T. mitchelli*) or with a single nerve with or without vestigial laterals visible in the lower part of the lemma; texture scarious, hardened, or horny-indurate; a minute callus at the base; hairs in a basal ring, a median dorsal series and a marginal fringe, these series varying in development from almost none to a complete cover of the entire part of the lemma, the lobes being glabrous or scabrid and usually ciliolate. *Palea* about as long as the entire base of the corresponding lemma but when the lemma is deeply lobed there may be a narrow tip which fits into the concavity of the middle lobe (Fig. 6(*b*)*H*, Fig. 9(*b*)*H*, Fig. 12(*c*)*H*); nerves scabrid or alate. The palea is commonly incurved over the floral organs but in some eastern Australian material the top may become slightly recurved. Lodicules cuneate or obovate. *Anthers* 3, often slightly twisted and dehiscing by subapical slits, purplish or brownish.

KEY TO SPECIES OF THE GENUS TRIODIA

A. Leaf sheaths 10-20 mm. wide at broadest point, laminae incurved-tubular, or flat when dry but not appearing terete. Spikelets 4-6 mm. long, panicles 30-60 cm. long. Lemma minutely 3-lobed.......................................1. ***procera***
AA. Leaf sheaths narrower than above, laminae appearing terete when dry owing to the conduplicate folding
B. Leaf sheaths thickened in the median third so that leafy culms appear flattened, usually resinous (except 5 and 6*b* below) or with a whitish incrustation of dried resin. Laminae striate along midrib on the under surface which is otherwise smooth
C. Spikelets up to 6 mm. long, very numerous along numerous lateral branches of the panicles which are 20-60 cm. long
D. Lemma with 3 minute teeth..............................2. ***microstachya***
DD. Lemma with 3 minute subulate lobes, the median one being twice as long...3. ***stenostachya***
DDD. Lemma divided to the middle into subequal subulate lobes....3a. ***cunninghamii***
CC. Spikelets more than 6 mm. long. Panicles smaller than above, spikelets not very numerous on the lateral branches
E. Spikelets narrow-linear, 7-14 mm. long, 2-3 mm. wide. Lemma glabrous except for very short basal hairs, rarely a few on lower back......4*a*. ***pungens*** var. ***linearis***
EE. Spikelets linear-lanceolate to ovate, more than 3 mm. wide
F. Lemma with short hairs, often scanty, arising from base, lower margin, and lower half of median line; closely distichous-imbricate; nerves obscure in entire part; lobes ¼-½ total length. Palea about as long as entire part...........4. ***pungens***
FF. Lemmas with silky hairs covering the lower half (if not hairy then lobes very short). Palea almost as long as total length of lemma, tip recurved except when very young
G. Lemmas loosely distichous when mature, nerves of lobes extending into entire part. Old leaves coiled.................................5. ***hostilis***
GG. Lemmas not loosely distichous, median lobe 5-nerved at base. Older leaves not coiled (*T. mitchelli* complex)
H. Scarious edge of the outer lobes of lemma, if present, not extending to base of lemma, which is always longer than broad
I. Spikelets dark purple (except when old). Lemmas with copious silky hairs arising from lower half of base. Lobes ⅓-½ total length......6. ***mitchelli*** var. ***mitchelli***
II. Spikelets pale or the glumes slightly coloured. Lemmas usually less hairy than above

J. Leaf sheaths resinous and more or less fringed with long hairs on the margins. Apex of lemma indented rather than lobed........*6a. mitchelli* var. *breviloba*

JJ. Leaf sheaths hirsute with long, soft hairs and with little or no resin. Lobing and hairiness of lemma variable............ 6*b. mitchelli* var. *pubivagina*

HH. Spikelets pale except for purplish glumes. Lemmas almost as wide as long, with a broad scarious margin extending from the lateral lobes to the base. Leaf sheaths resinous but glabrous.. ....7. *marginata*

BB. Leaf sheaths not resinous, not especially thickened in the median third so that culms are not laterally flattened. Laminae evenly striate on the under surface

K. Spikelets pedicellate in open or narrow panicles or along lateral branches, not spicate on main rhachis

L. Spikelets not conspicuously racemose or spicate along alternate lateral branches of the rhachis

M. Lobes of the lemmas stiffly scarious and as long as or longer than the horny base. Leaf sheaths more or less woolly, always woolly at the orifice

N. Lateral lobes of the lemmas obtuse or acute and glabrous except for marginal cilia..................... ....8. *basedowii*

NN. Lateral lobes of the lemmas acuminate and softly pubescent......9. *lanigera*

MM. Lobes of the lemmas never as long as the base and may be mere indentations of the apices, not scarious unless the whole texture is thin

O. Panicle very open with numerous spikelets on pedicels up to 2.5 cm. long. Glumes aristulate. Mid lobe of lemma up to twice as long as laterals.................. .. .. 10. *plectrachnoides*

OO. Panicle small or narrow though loose. Spikelets on shorter pedicels than above. Glumes acuminate, acute, or mucronate. Lobes of lemmas subequal or the mid lobe shorter

P. Lemmas lobed or tridentate, not emarginate. Nerves in lateral lobes of lemmas always central. Paleal nerves at least narrowly alate

Q. Orifice with bright or glistening, erect or spreading hairs which usually extend along the lower margins of the laminae

R. Lemmas lobed to $\frac{1}{3}$ of total length. Wings on nerves of palea narrow, sometimes visible but not conspicuous in spikelet....11. *wiseana* and var.

RR. Lemmas minutely tridentate. Wings on paleal nerves very conspicuous...................................... 12. *intermedia*

QQ. Hairs of orifice not as above

S. Hairs of orifice woolly or flaccid, tangled. Glumes 3-5-nerved

T. Lemmas with a dense fringe of hairs developed between the lateral nerve group and the margin of the entire part

U. Spikelets 7-10-flowered, 12-20 mm. long and 6-8 mm. wide 13. *brizoides*

UU. Spikelets 4-6-flowered, up to 10 mm. long and 3-5 mm. wide......................................14. *burkensis*

TT. Lemmas without a marginal fringe of hairs

V. Spikelets ovate to oblong, flattened laterally. Lobes of lemmas flattened at base. Palea with a narrow glabrous tip and the wings of the nerves visible in the spikelet ....15. *inutilis*

VV. Spikelets linear to lanceolate, plump. Lobes of lemmas subulate. Palea with minute apical tuft of hairs, the nerves narrowly winged ....16. *molesta*

SS. Hairs of orifice very short (less than 1 mm.). Glumes 1-nerved. Spikelets linear, 10-20 mm. long, 3-5 mm. wide. Lemmas very shortly lobed and with few short hairs at base and along median line........17. *longiceps*

PP. Lemmas emarginate, the lateral lobes thin and the nerve excentric, the mid lobe continued as a mucro or short awn. Nerves of palea not alate. Orifice hairs absent or very short except in *T. lanata* (*T. irritans* complex)

W. Central nerve of lemmas continued as a short awn between the stiffly scarious lateral lobes. Palea glabrous on back. Outer glumes as long as or nearly as long as spikelets.....................18. *irritans* var. *irritans*

WW. Central nerve of lemma short in an emarginate or ragged or semi-truncate apex. Outer glumes rarely more than half as long as spikelet, usually about as long as lowest lemma (if longer then the lemma is not aristulate). Palea hairy on back

X. Sheaths and glumes glabrous, puberulous, or scabrid

Y. Glumes and lemmas stiff and more or less indurate. Lateral portions of the lemmas flat and with a group of 2 or 3 distinct nerves

Z. Spikelets 8-12-flowered. Lemmas neatly distichous-imbricate. South coast and Victorian Mallee.................19. *irritans* var. *compacta*

ZZ. Spikelets 4-8-flowered. Opposing lemmas closely overlapping when young but later very loosely distichous and divaricate. Inland and eastern........ ....19*a*. *irritans* var. *laxispicata*

YY. Glumes and lemmas thinly scarious. Lateral nerve (or closely proximal nerves) forming a ridge above so that the lemma may appear dorsally flattened towards the apex.............. ....20. *scariosa*

XX. Leaf sheaths woolly tomentose. Glumes more or less pubescent 21. *lanata*

LL. Spikelets racemose or spicate and loosely or compactly secund along conspicuously alternate lateral branches of a narrow panicle

a. Lemmas with 3 groups of 3 nerves. Hairs of the leaf sheafs continued on to the petiole-like base of the laminae

b. Plants with scattered droplets of secretion. Sheaths conspicuously ciliate. Spikelets 3-4-flowered........... ....22. *roscida*

bb. Plants without secretion. Sheaths with white tomentum, not ciliate. Spikelets 5-8-flowered............. ....16. *molesta*

aa. Lemmas apparently 3-nerved though faint traces of the lateral members of the triplets may be found. Hairs of the leaf sheaths not continued on the petiole-like base of the laminae

c. Paleas winged on the nerves. Spikelets loosely or distichously secund

d. Lemmas indurate

e. Leaf-sheaths minutely puberulous. Spikelets more than 6 mm. long

f. Glumes 1-nerved. Lemmas minutely tridentate. Paleal wings protudent in upper half of floret....................................17. *longiceps*

ff. Glumes 3-nerved. Lemmas 3-lobed. Paleal wings narrow and concealed...23. *triticoides*

ee. Leaf sheaths villous pubescent with silky hairs. Spikelets 4.5-6 mm. long. Lemmas 3-lobed. Paleal wings narrow and concealed .....24. *racemigera*

dd. Lemmas scarious. Spikelets 4-6 mm. long. Sheaths minutely silky-pubescent with longer hairs on the margins.........................25. *fitzgeraldii*

cc. Paleas not winged on the nerves. Spikelets densely secund

g. Orifices with short erect hairs. Lemmas glabrous or with few basal hairs.... ....26. *angusta*

gg. Orifices with erect fringed appendages. Lemmas pubescent on back and along margin.......................................27. *secunda*

KK. Spikelets sessile and biseriate on main rhachis. Orifice with loose, flaccid hairs up to 4 mm. long, lemma acuminate..........................28. *spicata*

1. **Triodia procera** R. Br. in Prodr. Nov. Holl. 182 1810).

Holotype.—(Not seen), north coast, *R. Brown.* Given as "Arnhem S. Bay" by Bentham in Fl. Aust. 7: 607 (1878).

Plants large ("rather dense, yellowish tussocks . . . flowering culms up to 2 m. high"—*Blake* No. 17165; "forming huge tussocks"—*White*; "stems many feet tall"—Bentham in Fl. Aust. 7: 607 (1878). *Leaf sheaths* 4-7 cm. long, 1-2 cm. wide, glabrous, the specimens not showing the resin referred to by Bentham (loc. cit.) though reference is made to a sticky secretion in the field notes on Specht's material, loose and not fully encircling the sheaths above, slightly keeled, the distichous arrangement (especially where there are lateral branches) producing a flattened appearance. The line of the junction of sheath and lamina so distinct that it is almost an articulation. The auricular ridge of the orifice ciliate with short, silky hairs, which are continued round the back of the lamina, the ligule of similar hairs but in old leaves the outer series may disappear. *Laminae* up to 70 cm. long, about one-third as wide as sheath at orifice, without petiole-like bases but with thickened flanges on either side which permit the laminae to stand away at an angle; incurved, the very scabrid margins sometimes touching so that the leaves become tubular (but not conduplicate-terete as in other species). In the available material the upper parts of the laminae are split and the apices missing, but judging from immature leaves the tips are not very pungent. *Panicles* very large, 40-60 cm. long, the main rhachis striate, scabrid or scabridulous, with numerous slender lateral branches up to 18 cm. long on which the spikelets are racemose. *Spikelets* shortly pedicellate, very numerous (up to 30 on longer branches) overmature in available specimens but probably 4-6 mm. long and 3-4-flowered. *Glumes* stiffly scarious, oblong-lanceolate, acute, 3-4 mm. long; lower with 3 scabrid nerves but in *Blake* No. 17165 the lateral nerve on one side is faint while there are 2 nerves on the other; upper 1-nerved or with 1 lateral, slightly shorter than or equal to the lower glume. *Lemmas* hardened, lanceolate, 3-nerved with the laterals near the margin, glabrous except for marginal hairs from the base almost to the minute 3 lobes; lowest 3.5 mm. long. *Paleas* glabrous, narrowly winged on the nerves (Fig. 5 (*a*)).

This species stands somewhat apart from all others owing to the character of the leaves. However, it is undoubtedly related to *T. pungens* as well as to *T. microstachya* and *T. stenostachya*.

Distribution.—NORTHERN AUSTRALIA: Groote Eylandt, "very common on coastal sandhills," *C. T. White*, 25.x.1939; about 13° 6′ S., 132° 27′ E. "low quartzite ridge in *Eucalyptus* forest ± 90 m.," *S. T. Blake* No. 17165, 4.x.1946 (CANB, BRI); no locality, *R. Brown*, 1802(?), (NSW) (fragment of type?); South Bay, Bickerton I., "abundant on coastal dunes and on quartzite . . . forming clumps up to 8 feet diameter . . . Leaves dull green to reddish brown as dry (sticky secretion)," *R. L. Specht*, No. 529, 11.vi.1948 (CANB) (cf. Fig. 1A).

2. **Triodia microstachya** R. Br. in Prodr. Nov. Holl. 182 (1810); *Festuca microstachya* F. Muell., Veg. Chath. Is. 60 (1864); *T. microstachya* in Bentham, Fl. Aust. 7: 607 (1878) (in part).

Holotype.—(Not seen), north coast, *R. Brown*. Given as "Islands off Arnhem's Land" by Bentham in Fl. Aust. 7: 607 (1878).

Dense green tussocks 45-70 cm. wide and about as high, flowering culms to 1 m. (Blake). *Culms* glabrous (or viscid with resin from sheaths). *Leaf*

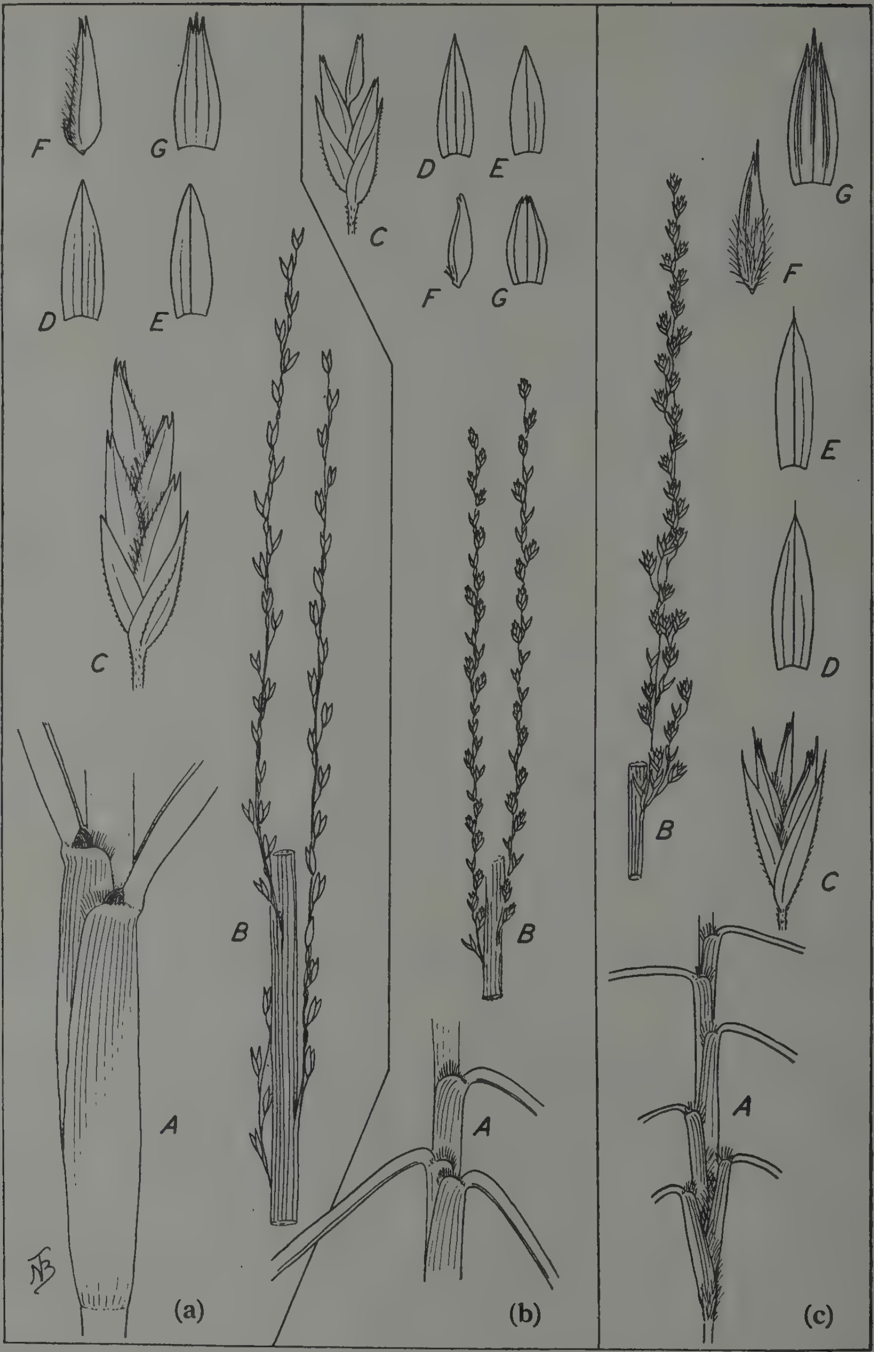

Fig. 5.—(*a*) *Triodia procera* R. Br., *A,B*, from *Specht*, No. 529; *C*, from *White*; *D,G*, from *Blake*, No. 17165. (*b*) *T. microstachya* R. Br., *A-G*, from *Specht*, No. 196. (*c*) *T. stenostachya* Domin, *A-G*, from *Blake*, No. 8158. *A*, portion of culm showing orifice of sheath (nat. size). *B*, portion of panicle with lateral branches (nat. size). *C*, spikelet × 5. *D*, lower glume × 5. *E*, upper glume × 5. *F*, lateral view of floret × 5. *G*, lemma, from within, × 5.

sheaths viscid, slightly keeled but not so flattened as in *T. pungens,* minutely striate, glabrous. The orifice with a fringe of hairs usually matted with resin as are also the hairs of the ligule, the orifice hairs extending around the back of the base of the lamina to the keel but shorter than those of the ridge. *Laminae* without a petiole-like base, about a third as wide as the sheath at the junction, viscid with resin especially towards the base but this may have come from the sheaths, the abaxial surface smooth laterally and with a median line of obscure, minute striations, conduplicate or more or less open and flat, the margins scabrid to the apex, the apices mostly broken and split, not strongly pungent (Bentham's reference to pungent-pointed leaves may have been based on those in Cunningham's specimen from the NW. coast which is now placed in *T. angusta*). *Panicle* large, 30-50 cm. long, the main rhachis and lateral branches very scabrid. *Spikelets* 4-5 mm. long, 3-4-flowered, very shortly pedicellate, racemose along the numerous, slender branches, which are up to 8 cm. long. *Glumes* oblong-lanceolate, stiffly scarious; lower 3-3.5 mm. long, 3-nerved but 2 nerves much more scabrid and inconspicuous than the third; upper 2.5-3 mm. long, 1-3-nerved but the laterals inconspicuous and none scabrid. *Lemmas* oblong-lanceolate, hardened, 2.53 mm. long, glabrous except for a few marginal hairs towards the base, 3-nerved, the median nerve usually and the laterals occasionally with an obscure nerve on either side, lobes minute and minutely ciliolate. *Paleas* glabrous, thin, slightly shorter than their lemmas, nerves minutely ciliolate, not winged (Fig. 5 (*a*)).

According to Blake the plants grow on the crests and slopes of stony hills but Specht found them on coastal dunes at Groote Eylandt.

Distribution.—NORTHERN AUSTRALIA: about SSE. of mouth of Daly River, 13° 51-53′ S., 130° 20-30′ E., S. *T. Blake,* No. 16614, 25.vii.1946; near Hayes Creek, 13° 35′ S., 131° 29′ E., S. *T. Blake,* No. 16179, 27.vi.1946; Katherine Gorge, 14° 19′ S., 132° 19′ E., S. *T. Blake,* No. 17206, 13.x.1946; Oenpelli, Northern Territory, "Clumps up to 4 feet diameter and 18 inches tall . . . flower spikes up to 3 feet tall," *R. L. Specht,* No. 1312, 31.x.1948; Little Lagoon, Groote Eylandt, "Abundant on coastal dunes . . . forming 'spinifex rings' up to 15 feet diameter . . . ," *R. L. Specht* No. 196, 9.iv.1948 (CANB) (cf. Fig. 1A).

3. **Triodia stenostachya** Domin in Bibl. Bot. 85: 387 (1915).

Holotype.—(Not seen), "am Castle Hill bei Townsville massenhaft", *Domin* II (1910).

Large tussocks up to 1-1.5 m. high (less in Queensland material) and 1-1.3 m. in diameter. *Culms* with tufts of branches where the internodes are short, the lower internodes sometimes pubescent below the nodes, upper nodes glabrous. *Leaf sheaths* resinous, especially towards the orifice, older sheaths with whitish incrustation of dried resin; thickened medianly and slightly keeled so as to give a flattened appearance to the branches, striate, margins of the lower sheaths on each shoot ciliate with silky hairs up to 3 mm. long, margins of the upper sheaths glabrous. Orifice with a fringe of hairs usually obscured by resin. *Laminae* glabrous, conduplicate, the abaxial surface minutely striate in the median line but smooth laterally, the apex slender and weakly pungent, margins smooth. *Panicles* up to 40 cm. long, spreading, rhachis scabrid. *Spikelets* 4.5-5 mm. long, shortly pedicellate and racemose along solitary or almost clustered scabrid branches of which the lowest are 7-10 cm. long, or in short racemes lateral to the branches. *Glumes* lanceolate, aristulate, equal or almost so, 3.5-4.5 mm. long, scarious or stiffly scarious, keeled; lower with 3 scabrid nerves, the laterals sometimes less distinct; upper with median nerve only or with 1 faint lateral. *Lemmas* 3-4, scarious or stiffly scarious, 3-3.5 mm. long, the apex tridentate, the median lobe more subulate than and twice as long as the laterals, which are not particularly divergent; nerves obscure in the basal part but visible above as the groups of 3 nerves converge into their respective lobes; with scanty hairs along the nerves in the lower half but the hairs not conspicuous in the spikelets. Callus short, blunt, glabrous. *Palea* linear or elliptical, 2.5-3 mm. long, glabrous except along the ciliate nerves. *Anthers* 1.5-1.75 mm. long. Grain not seen (Fig. 5(*c*)).

Distribution.—Northern Australia from the Kimberley District in Western Australia to Queensland. WESTERN AUSTRALIA: Ord River Gorge, *C. A. Gardner*, No. 7337, 5.vi.1944 (BRI). QUEENSLAND: Magnetic I., near Townsville, *S. T. Blake*, No. 8236, 24.iii.1935 and No. 8262, 26.iii.1935; Townsville on exposed rocky slopes of Castle Hill, *S. T. Blake*, No. 8158, 22.iii.1935 and No. 5934, 7.vi.1934; Chillagoe, *S. T. Blake*, No. 14746, 26.xi.1942; North Kennedy District, Castle Hill, Townsville, *D. A. Goy*, No. 379, 25.vii.1938 (BRI, CANB).

3a. **Triodia cunninghamii** Benth. in Fl. Aust. 7: 606 (1878).

Lectotype.—Cambridge Gulf, NW. Coast, *A. Cunningham.*

In the study of the Western Australian species (Burbidge 1946*a*) the statement was made that *T. cunninghamii* Benth. could not be distinguished from *T. pungens* R.Br. This was based on certain small-spikeleted forms collected by the author on the 80-Mile Beach north of the De Grey River. Later in the year of publication Mr. C. A. Gardner, Government Botanist for Western Australia, collected specimens in the Kimberley district, which were quite distinct from *T. pungens* and which appeared to agree with Bentham's description of *T. cunninghamii.* As his material was collected near to but south from Cunningham's type locality the identity seemed fairly definite. Subsequently the specimen was checked in Brisbane, where it was found to agree in many respects with Queensland material determined as *T. stenostachya* Domin. Consequently in his Flora of Western Australia:Gramineae, Gardner (1952) reduced Domin's name to a synonym.

However, recent comparison of Queensland specimens of *T. stenostachya* with Cunningham's specimens at the Kew Herbarium shows that they are not quite the same. In Domin's species the lemmas are shortly tridentate and by no means "divided nearly to the middle" as Bentham describes them in *T. cunninghamii.* In the type material many of the lemmas have been lost but in apparently undamaged ones amongst those remaining the lobes are equally subulate and quite as long as the base. Also the glumes are chartaceous in texture and elliptical in outline rather than scarious and lanceolate as seems characteristic in *T. stenostachya.* Consequently Domin's name should be reinstated. A re-description of Cunningham's material follows:

Foliage similar to that of *T. pungens. Leaf sheaths* resinous but less so on stolons where the margins may be fringed with woolly hairs. *Panicle* up to at least 30 cm. long (detached and apparently incomplete on all type material), narrow when dry. *Spikelets* 5-6 mm. long, ellipsoid, shortly pedicellate along numerous lateral branches irregularly arranged along the angular rhachis. *Glumes* elliptical or ovate-elliptical, firm in texture, minutely scabridulous; lower 5.5 mm. long, 3-5-nerved, upper 4.5 mm. long, 3-nerved, in both the scabrid mid nerve continued as a short awn 0.5-0.75 mm. long above the acute or almost obtuse apex which is commonly torn along the lines of the nerves. *Lemmas* short and with the awns barely protruding above the glumes, hairy on the entire base, lobed to the middle; lobes subequal, subulate, slightly spreading, apparently brittle, and in many cases broken off short (where only the laterals are broken the resemblance to *T. stenostachya* is increased). *Palea* as long as or slightly longer than entire portion.

Gardner's description (loc. cit., p. 73) matches this better than it does Domin's text though his figure of the lemma is closer to that of *T. stenostachya.* Presumably both are largely based on his No. 7337, from the Ord River gorge, which was not available for restudy during the final stages of compilation.

Bentham listed 2 specimens, the first collected in Cambridge Gulf by Cunningham and the second from Suttor Desert and collected by Mueller of which Bentham says "apparently the same as Cunningham's plant, but only a single specimen seen." There seems to be no doubt that Cunningham's specimen must be regarded as the type. In the Melbourne Herbarium there is a sheet bearing a piece of culm with 2 leaves and a capsule containing a fragment of panicle. According to the label this was collected in the Suttor Desert by Mueller and it is presumably portion of the Suttor Desert material still held at Kew as that seen by Bentham. On this specimen the panicle is small (10-12 cm. long) and the lemmas differ in having flattened lobes with ciliate margins. The paleas have a narrow tip which is sometimes recurved. This plant seems to be distinct from both *T. cunninghamii* when the name is strictly applied to Cunningham's specimens and from Domin's species. In point of fact there is a closer analogy with *T. mitchelli* where the recurved tip to the palea is characteristic but the spikelets are always larger.

As understood here the species rests on Cunningham's material at Kew and possibly should include Gardner's No. 7337 quoted above under *T. stenostachya.*

4. **Triodia pungens** R. Br. in Prodr. Nov. Holl. 182 (1810); C. E. Hubbard in Hook. Ic. Pl. 4 (ii). Plate 3336; N. T. Burbidge in J. Roy. Soc. W. Aust. 30: 21 (1946) (in part); *T. viscida* Roem. & Schult., Sys. Veg. ii: 599 (1817); *Festuca viscida* F. Muell. in Veg. Chath. Is. 59 (1864); *T. vulnerans* Domin in Bibl. Bot. 85: 385-6 (1915).

Holotype.—North coast, *R. Brown.* Given as "Islands of the Gulf of Carpentaria" by Bentham in Fl. Aust. 7: 606 (1878).

Leaves with resinous sheaths thickened along the median line so that the leafy culms appear flattened. The resin is developed from secretory cells in the thinner marginal portions (Burbidge 1946*a*) and this resiniferous tissue may extend on to the base of the laminae. Resin found in other parts of the plant has usually resulted from contact with the sticky sheaths. The internal structure of the laminae has been described elsewhere (loc. cit.). The abaxial surface is smooth except along the median line where there are minute striations corresponding to the grooves between the nerves (Fig. 6(*a*)*A′*). The adaxial surface is striated, the grooves being deeper on either side of the mid nerve. The orifice has glistening hairs which are commonly matted with resin. *Panicles* loosely pyramidal at anthesis but in herbarium material the branches are usually erect and the panicle relatively compact, 10-30 cm. long, the lateral branches bearing more or less pedicellate spikelets which, when numerous, may be racemosely arranged. There are pulvini at the bases of the branches (Burbidge 1945*b*, Plate 22, Fig. 4), which are responsible for the change in their positions at anthesis. *Spikelets* linear or linear lanceolate though if the rhachilla joints are very short they may be ovate. *Glumes* stiffly subscarious or indurate, subequal and 5-7-nerved, boat-shaped or oblong to lanceolate, the apex usually acute but varying from obtuse to long-acute, usually pale in colour. *Lemmas* deeply 3-lobed, broad, the lateral lobes broad at the base and subulate at the tips while on either side there is a thinner flap that extends from the lateral lobe down the upper part of the margin of the entire portion, which is hardened or yellowish-indurate and horny. The nerves are conspicuous in the lobes owing to associated bands of chlorenchyma but are quite obscure in the entire portion. The whole lemma may be almost glabrous except for very short silky hairs at the base near the short callus or there may be a line of hairs extending up about half of the median line as well as hairs along the lower part of the margin. The lobes are ciliolate. Lowest lemma 5-8 mm. long (shorter in variety). *Palea* about as long as or a little longer than the entire portion of its lemma, incurved over the floral organs, apex ciliolate and, in Queensland specimens, sometimes with a narrow tip, which fits into the concave central lobe of the lemma; nerves narrowly winged (Fig. 6(*a*), (*b*)).

As can be seen in Figure 1*B* the species covers a very wide range and some variation is only to be expected. Variation of the plants in the field in Western Australia has already been discussed (Burbidge 1946*a*) and with this in mind it has not seemed advisable to split the species other than to describe the variety given below. This leaves a range of forms including that on which Robert Brown based his species. It does not appear that any useful purpose will be served by subdividing and no variety based on Robert Brown's material is designated.

In Western Australia a form, in which the lemmas have a very horny base sharply demarcated from the stiffly scarious lobes, is restricted to the Pilbara region so far as is at present known (Fig. 6(*b*)). This character is lacking from the material collected in the Kimberleys. It would have been suitable as a varietal character but as the plants show so much variation in the field in regard to other features the separation has not been made (Burbidge 1946*a*). The thickening is similar to that found in *T. lanigera* and *T. basedowii*, of which the former is common in the same area and it seems possible that there may

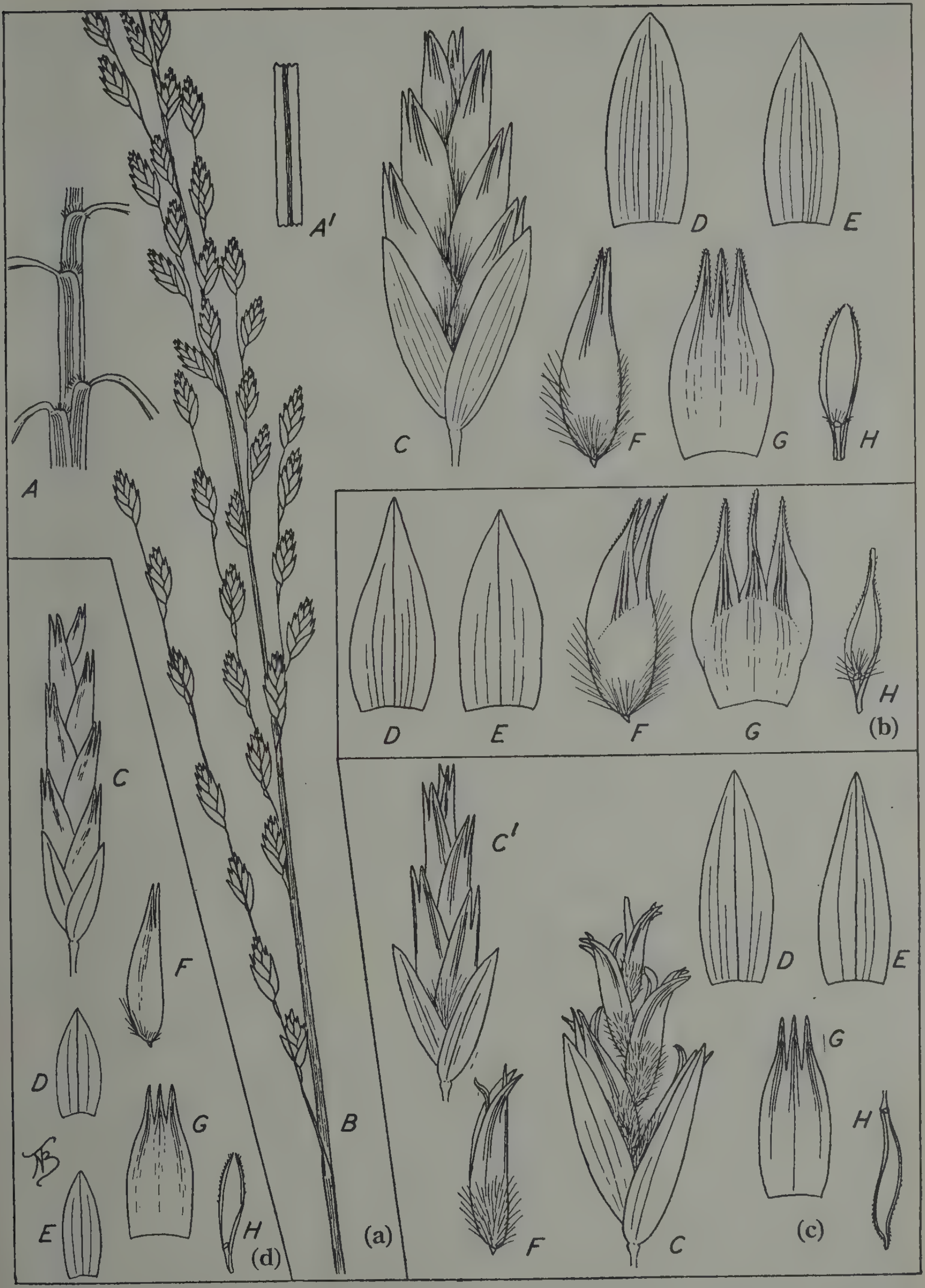

Fig. 6.—(*a*) *Triodia pungens* R. Br., from *Blake*, No. 10244. (*b*) *T. pungens* R. Br., Pilbara form, from *Burbidge*, No. 1621. (*c*) *T. hostilis* Domin, *C-H*, from *Blake*, No. 15325, *C′* from Domin material at Sydney. (*d*) *T. pungens* var. *linearis* var. nov., from *Perry*, No. 547. Lettering as in Figure 5 except that *A′* is part of the lamina showing appearance of abaxial surface and *H* = palea, abaxial view (upside down).

have been some interbreeding in the past. The Pilbara form is approached by some specimens from the Northern Territory (e.g. *Blake* No. 17870) though there is not the same break in texture at the base of the lobes.

On the other hand the eastern specimens show, through *T. hostilis,* a definite relationship with *T. mitchelli* sens. lat., while the northern material from between the Kimberleys and northern Queensland tends to have more evenly indurated lemmas which are slender in shape and commonly glabrous except for the short basal hairs. This last group includes the specimen labelled as co-type, collected by Robert Brown, which is in the Sydney Herbarium. In Brown's material the lemmas have rather shorter lobes than is usual in the rest of the material but this character seems to vary considerably. Throughout the range the lobes of the lemmas vary from flat to almost subulate.

Distribution.—WESTERN AUSTRALIA: Pilbara region (additional to specimens quoted in Burbidge 1946*a*), 9 miles S. of Port Hedland, *C. M. Donald,* Oct. 1946 (CANB); Port Hedland, *W. V. Fitzgerald,* July 1906; Port Hedland and Broome, *W. V. Fitzgerald,* Apr. 1905; Condon, in the vicinity of the Rabbit Proof Fence, *Crawford,* June 1912; NW. Australia, *Crawford,* 1909 (NSW). Kimberley district, 13 miles S. of Lissadell Station, *R. A. Perry,* No. 2675, 3.viii.1949; 60 miles N. of Turkey Creek Police Station, *R. A. Perry,* No. 2534, 19.vii.1949; 22 miles S. of Gordon Downs Station, *R. A. Perry,* No. 2485, 14.vii.1949; 10 miles NE. of Gordon Downs Station, *R. A. Perry,* No. 2450, 13.vii.1949 (CANB). CENTRAL AUSTRALIA: Mount Liebig, *J. B. Cleland,* Aug. 1932 (immature—spikelets not quite typical) (BRI). Napperby, 100 miles NW. of Alice Springs, *S. L. Everist,* Nos. 4181, 4216, 4221, 24-26.i.1950. NORTHERN TERRITORY: 13 miles SW. of Wave Hill Station, *R. A. Perry,* No. 2201, 21.vi.1949; 30 miles SW. of Victoria Downs Station, *R. A. Perry,* No. 2171, 18.vi.1949 (CANB); Tanami, Warden of Tanami per *R. S. Rogers,* Aug., Sept. 1910 (NSW); 27 miles W. of The Granites, Chief Veterinary Officer, July 1948; ½ mile N. of Tennant Creek township, *R. A. Perry,* No. 583, 25.iv.1948; headwaters of Kilgour R., 17° 11′ S., 135° 45′ E., *S. T. Blake,* No. 17773, 14.v.1947; Rockingham Downs Station, 19° 2′ S., 135° 9′ E., *S. T. Blake,* No. 17870, 19.v.1947; W. to SW. of Soudan Station, 19° 50′ S., 136° 5′ E., *S. T. Blake,* No. 15978, 16.vi.1946; 59 miles W. of Gallipoli Station (part of Alexandria Station), *R. A. Perry,* No. 1531, 15.vi.1948; 22 miles E. of Alexandria Station, *R. A. Perry,* No. 1499, 23.vi.1948; 75 miles SW. of Lake Nash Station, *R. A. Perry,* Nos. 879 and 880, 21.v.1948; 76 miles SW. of Lake Nash Station, *R. A. Perry,* No. 889, 21.v. 1948 (CANB); "CO-TYPE" material collected *Robert Brown* distributed *J. J. Bennett* 1876 (NSW). QUEENSLAND: 5 miles E. of Corinda Station, *R. A. Perry,* No. 1377, 6.vi.1948; 61 miles N. of Lawn Hill, *R. A. Perry,* No. 1141, 1.vi.1948; 54 miles N. of Lawn Hill Station, *R. A. Perry,* No. 1136, 1.vi.1948; 50 miles N. of Lawn Hill Station, *R. A. Perry,* No. 1122, 1.vi.1948; 25 miles N. of Lawn Hill Station, *R. A. Perry,* No. 1109, 31.v.1948; 35 miles W. of Gregory Downs Station, *R. A. Perry,* No. 1412, 9.vi.1948; 18 miles W. of Gregory Downs Station, *R. A. Perry,* No. 1410, 9.vi.1948; 4 miles SSE. of Barkly Downs Station, *R. A. Perry,* Nos. 741 and 742, 4.v.1948; 20 miles S. of Mount Isa, *R. A. Perry,* No. 777, 9.v.1948; 22 miles NE. of Headingly Station, *R. A. Perry,* No. 849, 19.v.1948; 24 miles E. of Urandangi, *R. A. Perry,* No. 829, 15.v.1948 (CANB); Cumberland, Gilbert River, *L. J. Brass,* No. 8840, May 1937 (BRI); Flinders River, *S. Browne,* Feb. 1914 (NSW); Duchess, *S. T. Blake,* No. 11516, 18.v.1936 (BRI); Mitchell district, Torrens Creek, *C. T. White,* No. 8787, 20.iii.1933; S. of Pentland on Milray Station, *S. T. Blake,* No. 9972, 22.x.1935 (BRI, CANB); among boulders on slopes of Mount Bowen, *S. T. Blake,* No. 12639 (BRI); Tulmur Station, approx. 22° 30′ S., 142° 25′ E., *S. T. Blake,* No. 11452, 11.v.1936 (BRI, CANB); Mitchell district, Corona Station, 50 miles W. of Longreach, *S. L. Everist,* N. 1506, 14.ii.1936; Mitchell district, Delta South, 30 miles SE. of Barcaldine, *S. L. Everist,* No. 1487, 7.ii.1936; Booroora, W. of Yalleroi, *S. L. Everist,* No. 1473, 14.xii.1935; near Yalleroi, *S. L. Everist,* No. 2029, 25.ii.1940

(BRI); Jericho, 300 miles W. of Rockhampton, *R. Simmons*, Jan. 1908 (NSW); E. of Jericho, *S. T. Blake*, No. 6834, 16.vii.1934 (BRI, CANB); Emerald, *R. Simmons*, No. 79, Feb. 1903 (NSW).

4a. **Triodia pungens** var. **linearis** var. nov.

Holotype.—8.5 miles N. of Tennant Creek, *R. A. Perry*, No. 549, 24.iv.1948.

Culmi et *folii T. pungenti* similes. *Panicula* gracilis, rhachis laeves, rami ad 4 cm. longi. *Spiculae* breves pedicellatae, lineares, 5-6-floriferae, 7-14 mm. longae, 2-3 mm. latae. *Glumae* oblongae, glabrae, scariosae, obtusae, subaequales, 2.5-3 mm. longae; 3-nervis (raro 5-7-nervis), medio prominente. *Lemmata* indurata, glabra, sed ad basim sparsim pubescentia (carina infra medium raro exiguissime pubescente), trilobata; lobis erectis, anguste subulatis, subaequalibus, vel medio lobo longiore; infima 3-4 mm. longa, 1.75-2 mm. lata. *Paleae* oblongae, 3 mm. longae, nervis anguste alatis, alis ciliolatis. *Antherae* 0.75 mm. longae, purpurascentes.

This variety differs in the much smaller and very narrow spikelets whose lemmas are almost glabrous. The panicle is also more slender and is longer in proportion to its width than that of *T. pungens* sens. str. The lobes of the lemma are not so long in relation to and are usually about a quarter of the total length but there is a similar thin margin. It may prove to be a relatively localized variation.

Distribution.—NORTHERN TERRITORY: 7.7 miles N. of Tennant Creek, *R. A. Perry*, No. 547; 8.5 miles N. of Tennant Creek, *R. A. Perry*, No. 549 (HOLOTYPE). Both collections 24.iv.1948. 30 miles N. of Helen Springs Station, *R. A. Perry*, No. 1889, 12.viii.1948 (CANB).

No. 547 bears the following note: "Tussocks several feet wide, one foot high. Panicle to three feet, on stony rise." No. 549 is "Hard tussock grass in small tussocks 9 inches high and 12 inches diameter, on very stony soil on pre-cambrian rocks." In No. 1889 the spikelets are slightly larger than in the other two specimens.

5. **Triodia hostilis** Domin in Bibl. Bot. 85: 387 (1915).

Holotype.—(Not seen). "Sandhügel der Dividing Range östlich von Pentland," Domin III (1910).

This species is not a very satisfactory one. It seems to combine a number of the characters of *T. pungens* on the one hand and *T. mitchelli* on the other. On these grounds hybrid origin could be suggested but without more information this cannot be assumed. It might be better as a variety but doubt is felt as to whether it is closer to *T. pungens* or to *T. mitchelli.* Consequently the author has decided to maintain Domin's name pending further investigation.

According to Blake's note on No. 15326, the plants are "broad rather rambling, low, green tussocks, culms ascending, branched, flowering ones 1½-2½ feet high. *Culms* and *leaves* similar to those in *T. pungens* except that the sheaths are only slightly resinous and that the laminae of the older leaves become coiled when dry. The latter character is also seen in occasional specimens of *T. pungens.* Owing to the lack of resin the hairs of the orifice are free and spreading. *Panicles* 10-20 cm. long, with slender lateral branches bearing pedicellate spikelets but sometimes bare towards the base. The rhachis is scabrid. *Spikelets* linear or almost cuneate when the glumes are long and spreading, 8-12 mm. long, 5-6-flowered, pale or the glumes and the lobes of the lemmas slightly tinted and purplish. In the fragment of Domin's specimen, held at Sydney, the lemmas are still tightly imbricate, giving a somewhat cylindrical appearance, but in the other specimens quoted below the lemmas are loosely distichous and divergent, whereas in *T. pungens* and *T. mitchelli* sens. lat. they are distichous-imbricate but not divaricate. *Glumes* oblong and obtuse to lanceolate, acuminate, when short the ciliolate apices sometimes slightly 3-lobed, subequal or equal, 5-8 mm. long, stiffly scarious, with 3 distinct nerves and sometimes a smaller one on the outside of the laterals, glabrous or scabrid on the nerves. In Domin's specimen the glumes are very shortly pubescent towards the base but this character is not mentioned in his description. *Lemmas* linear-lanceolate, lowest 4-5 mm. long, 2 mm. wide, lobed to a third of the total length, the lobes narrow, erect, and obtuse, the whole texture stiff but less indurate than in *T. pungens* and without a distinct and thin margin extending down from the lateral lobes, the nerves conspicuous in each lobe and visible almost to the base of the entire portion which is softly pubescent below and glabrous above except that the lobes are ciliolate. The callus is short, obtuse, and almost glabrous or shortly hairy. *Palea* longer than the entire base of the lemma but ending a little below the tips of the lobes, the apex often recurved as in *T. mitchelli* sens. lat., the nerves very narrowly alate and ciliolate (Fig. 6(*c*)).

On the basis of the original description it is not easy to separate this from either *T. pungens* or *T. mitchelli* var. *mitchelli.* Its relationship with the former is evident from the general appearance and the pale spikelets but the hairiness of the lemma, its nervation, and the recurved tip of the palea point to a close affinity with *T. mitchelli* var. *mitchelli.*

Distribution.—QUEENSLAND: "incolle arenaceo montium Dividing Range prope opp. Pentland," *Domin* III, 1910 (NSW); Pentland, *S. T. Blake,* No. 8386A, 1.iv.1935 (not a good match for Domin's specimen—N.T.B.) (BRI, CANB); Mitchell district, Torrens Creek, *C. T. White,* Nos. 8788 and 8789, 20.iii.1933 (BRI); Canoona, *c.* 30 miles NNW. of Rockhampton, *S. T. Blake,* Nos. 15235 and 15236, 22.ix.1943 (BRI, CANB); Expedition Range, *Thozet,* 1878 (MEL); Port Curtis district, Marlborough, *C. T. White,* 27.x.1937 (BRI).

6. **Triodia mitchelli** var. **mitchelli** (Benth. sens. orig.) comb. et stat. nov.; *T. mitchelli* Benth. in Fl. Aust. 7: 606 (1878); *T. pungens* Lindl. non R. Br.

Syntypes.—On the Maranoa, *Leichhardt,* near Mt. Pluto, *Mitchell.*

Forming dense tussocks to 1.5 m. high. *Culms* glabrous. *Leaf sheaths* usually resinous, the exposed sheaths below the panicles less so than those on vegetative shoots but sometimes with resin near the exposed nodes. Orifice with shining hairs like those in *T. pungens* but often longer, more or less tangled with resin, and extending to the slight keel on the abaxial surface of the junction. *Laminae* as in *T. pungens* but the margins more scabrid. *Panicle* open and pyramidal though the branches are more or less erect in dried material,

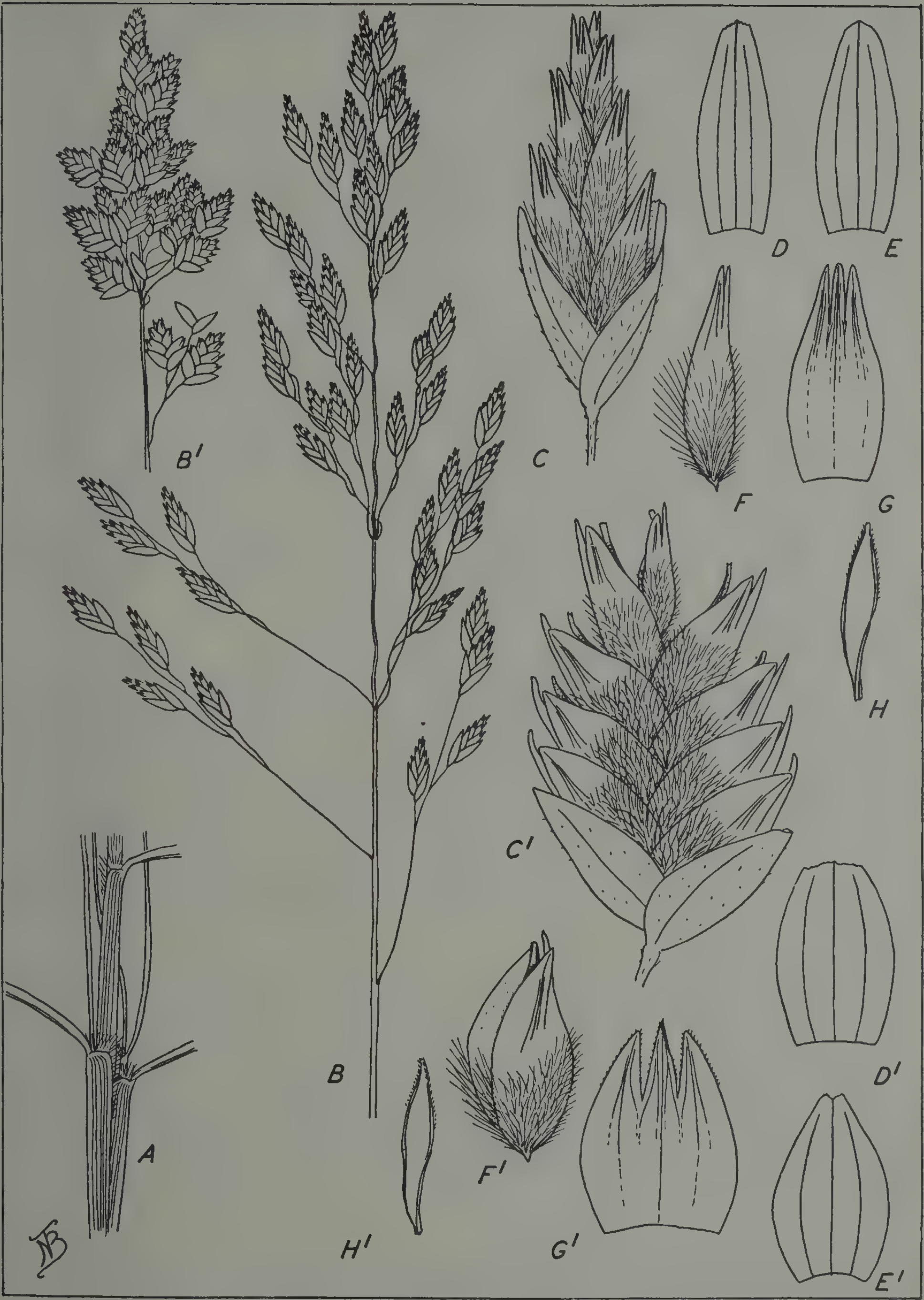
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Fig. 7.—*Triodia mitchelli* var. *mitchelli, A-H,* from *Blake,* No. 6968, *B'-H'* from *Kneebone,* 18.viii.1948. Lettering as in Figures 5 and 6.

rhachis scabrid to scabrid-pubescent and slightly resinous. *Spikelets* 5-9-flowered, linear to lanceolate and loose owing to the length of the rhachilla joints or compact and ovate-oblong if the joints are short; on slender pedicels, 4-6 on longer branches. *Glumes* dark purple except when faded with age, broadly lanceolate, subequal or equal, 5-7.5 mm. long, 1.75-2.5 mm. wide; lowest 3-nerved, nerves scabrid, apex acute-acuminate or obtuse and ciliate or the 3 nerves forming 3 minute teeth; upper 3-nerved, with or without several minor nerves in the upper half, apex acute-acuminate to slightly emarginate. *Lemmas* 5-8 mm. long, 2.5-4.5 mm. wide, deeply 3-lobed (to almost half total length), entire base pale-coloured, stiff or hardened, obscured by soft hairs which arise mainly from the short callus and from the margin and back of the lemma but usually cover the lower part; lobes erect or spreading, purplish to dark purple, minutely scabridulous, subequal or the median one slightly longer, acuminate or the laterals obtuse, 3 nerves visible in each lateral lobe but the middle lobe with an additional nerve on either side of the central group so that the base of the lobe is 5-nerved (Fig. 7*G′*), all nerves obscure below; margin of the lateral lobes thin and scarious but the border not extending to the base of the lemma and not very conspicuous. *Palea* glabrous or with a few hairs towards the base, nerves very narrowly winged, wings entire or minutely ciliolate, at the apex abruptly narrowed into a glabrous beak, 1-1.5 mm. long and thinner in texture, fitting into the concavity of the median lobe of the lemma but free and recurved in many specimens (Fig. 7).

The above description has been based on the full range of material quoted but it is admitted that many of the specimens do not match the type material very closely. Indeed there is no fully satisfactory match among the more recently collected specimens. On Mitchell's material the spikelets are slightly larger, being up to 20 mm. long (as compared to up to 16 mm.) and the lemmas are more numerous and more villous. While the differences are striking in the extremes, closer study of the range shows them to be quantitative rather than qualitative and, there being no sharp lines of demarcation at any particular point or points between the various forms included in the variety, subdivision appears to be impracticable.

This variety is quite distinct from the plants described below under varietal names, except for some of the specimens listed under var. *pubivagina* where the spikelets are always pale so far as is known. Var. *pubivagina* includes specimens that appear to bridge the gap between var. *mitchelli* and var. *breviloba* as well as the gap between var. *mitchelli* and var. *pubivagina* itself. The last-named, resting as it does, on the colour of the spikelets and the hairiness of the sheaths, cannot be regarded as a well-differentiated group. The relationships between the variations appear to be too complex to resolve on the basis of herbarium material alone.

Distribution.—QUEENSLAND: Central Queensland to the New South Wales border. Mitchell district, Torrens Creek, *W. Chisholm*, Aug. 1933. also *A. F. Moodie*, 12.vii.1934; also *C. T. White*, No. 8785, 20.iii.1933 (BRI); W. of Portland, between Warrigal and Burra on slopes of Great Dividing Range, *S. T. Blake*, Nos. 9944 and 9945, 19.x.1935; S. of Pentland on Milray Station on sandy slopes of Crooked Creek, *S. T. Blake*, No. 9973, 21.x.1935;

between Jericho and Lochnagar, *S. T. Blake*, No. 6869, 17.vii.1934 (BRI, CANB); Jericho, 300 miles W. of Rockhampton, *R. Simmons*, No. 53, Jan. 1908 (NSW); Alpha-Jericho, *U. Kneebone*, 18.viii.1948 (NSW); top of Great Dividing Range, E. of Jericho, *S. T. Blake*, Nos. 6841 and 6843, 16.vii.1934 (BRI, CANB); Boorara, about 6 miles W. of Yalleroi (SW. from Jericho), *S. L. Everist*, No. 1841, 24.vi.1939; 5 miles E. of Yalleroi, *L. S. Smith and S. L. Everist*, No. 941, 22.x.1940; Enniskillen, among sandstone rocks, base of Sugarloaf Mt., *C. T. White*, No. 12745, 14.xi.1943; Sandhurst Park, Fernlees (S. of Emerald), *J. Garvey*, No. 7, Sept. 1933 (BRI); Minerva, N. of Springsure, *S. T. Blake*, No. 6968, 22.vii.1934 (BRI, CANB); Leichhardt district, Carnarvon Range between Roma and Springsure, *C. T. White*, No. 9481, 26.iii.1933 and No. 11381, 26.ix.1940 (BRI); Maranoa, *Leichhardt* (SYN-TYPE) (MEL); tropical New Holland; *Sir Thomas Mitchell*, No. 474, 1846 (SYN-TYPE?) (NSW).

6a. **Triodia mitchelli** var. **breviloba** var. nov.

Holotype.—Cumborah, *N. Beadle*, Feb. 1942.

Foliorum vaginae resinosae, marginibus hirsutis vel glabrescentibus. *Spiculae* pallidae, pedicellatae, lanceolatae, 7-12 mm. longae, 2.5-5 mm. latae, 5-9-floriferae. *Glumae* pallidae, oblongae vel lanceolatae, obtusae vel acutae, subaequales, 4.5-5.5 mm. longae, glabrae, 3-nervis: *Lemmata* ovata vel lanceolata, ad apicem tridentata, lobis obtusis, erectis vel incurvis, nervatis, ad basim leviter pubescentia. *Paleae* ellipticae, membranaceae, nervis anguste alatis, alis ciliolatis.

Leaf sheaths less resinous than in var. *mitchelli*, orifice fringe extending for a variable distance down the margins of the sheath. *Laminae* as in var. *mitchelli*. *Panicle* more compact, the shortly pedicellate spikelets on short lateral branches 1-4 cm. long. *Spikelets* lanceolate, laterally flattened but well filled, 7-12 mm. long, 2.5-5 mm. wide, pale. *Glumes* oblong or oblong-lanceolate, obtuse or shortly acute, each with 3 conspicuous nerves but the lower with a lesser nerve near the margin, the upper with 1 or no lesser nerves. *Lemmas* 4-5 mm. long, 2.5-3 mm. wide, ovate or broadly lanceolate, hardened, very shortly 3-lobed, lobes linear, obtuse or acute, the median one equal to or shorter than the laterals, entire portion of lemma 9-nerved with the 3 groups of 3 nerves each rather more evenly distributed than in related varieties and with a faint additional nerve on either side of the central group, the upper part of the lemma appearing slightly striate under a lens, the nerves converging into the lobes. The lemmas are shortly silky pubescent in the lowest third or almost glabrous except along the median line in the lower third. Callus short and silky pubescent. *Palea* 3.5-4.5 mm. long, elliptical, the tip often slightly recurved. *Anthers* 3, dehiscing from apical pores or slits (Fig. 8(*a*) *B-H*).

The pale, very shortly lobed lemmas make this a very distinct variety. Except for the range of variation shown by the specimens grouped under the var. *pubivagina* below this would have been described as a distinct species.

Distribution.—QUEENSLAND: Balonne near Dirranbandi, *A. B. Cashmore*, 24.ix.1936 (CANB); Balonne River near Dirranbandi, *R. Roe*, No. 9, 29.ix.1936 (BRI); Toulby Gate, Queensland/N.S.W. border, *R. Roe*, No. AR219, 13.x.1949. NEW SOUTH WALES: Bourke district, O. C. McDougall, 1901; on sandhills between Cumborah and Llanillo, County of Finch, *Mullens*, 8.xii.1916; Cumborah, N. Beadle, Feb. 1942 (HOLOTYPE); north-west of N.S.W., S. W. Jackson, Oct. 1911 (NSW).

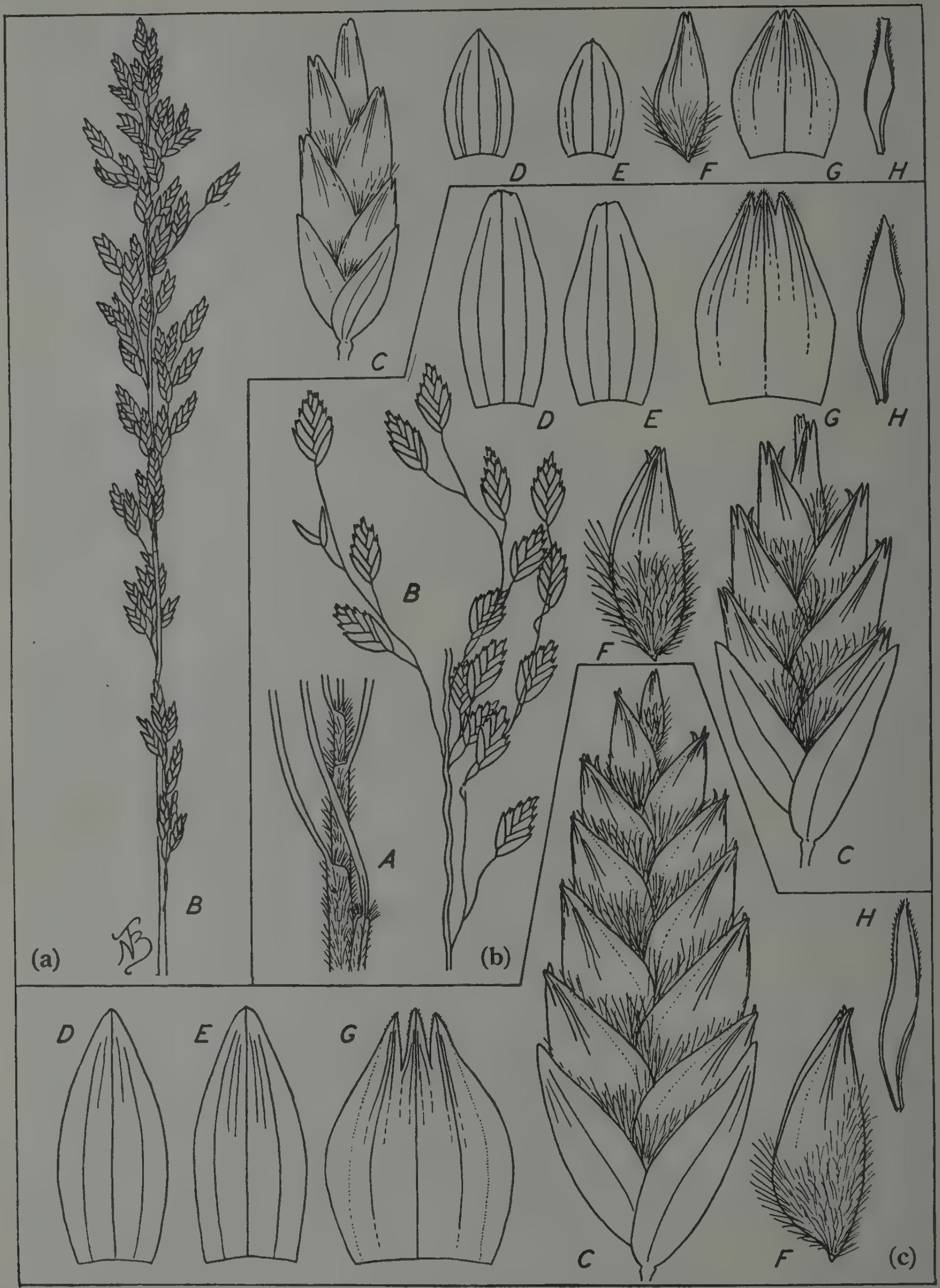
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Fig. 8.—(*a*) *Triodia mitchelli* var. *breviloba* var. nov., from *Beadle,* Feb. 1942. (*b*) *T. mitchelli* var. *pubivagina* var. nov., from *Boorman,* Nov. 1910. (*c*) *T. marginata* sp. nov., from *Baker,* No. 865. Lettering as in previous figures.

6b. **Triodia mitchelli** var. **pubivagina** var. nov.

Holotype.—Narrabri, *J. L. Boorman,* Nov. 1910.

Foliorum vaginae non resinosae, dense hirsutae. *Spiculae* pallidae, pedicellatae. *Glumae* pallidae vel purpurescentes. *Lemmata* pallida, trilobata vel tridentata, lobis erectis vel recurvis, ad basim pubescentia. *Paleae* ellipticae, membranaceae, apices angustae.

Spikelets variable in colour, usually pale and when purplish merely slightly so and not dark purple as in var. *mitchelli. Glumes* lanceolate, obtuse to acute. *Lemmas* vary in depth of lobing from tridentate as in var. *breviloba* to deeply lobed as in var. *mitchelli.* In some specimens very few lemmas (3-4) are present and these do not protrude above the glumes. This character has a very marked effect on the general appearance of the specimen but, at least in some cases, it may be due to immaturity.

Owing to the fact that a range of variations have been included in this variety it is less easy to describe than are the other members of the complex. The most consistent character is the practically non-resinous but densely hirsute leaf sheaths, the hairs being soft and loosely appressed. While vegetative characters are seldom reliable for diagnostic purposes, the character of the leaf sheaths and (more particularly) the hairs of the orifice have proved to be very useful in *Triodia.* This it does not seem unreasonable to employ the leaf character to differentiate this variety though, at the same time, it is felt that the specimens listed below are too heterogeneous to constitute a completely natural group.

Attached to Boorman's Narrabri material, which has been selected as a type for the variety and is figured in Figure 8(*b*) *A-H*, there is a set of accompanying notes, which include the following: "grows to about 5 feet high when in flower. The habit of the plant is not to spread itself on the ground forming large globular shaped plants as in *T. irritans.* It lifts itself from the ground forming a loose perpendicular habit, its leaves run in the same direction as the panicle, not pendulous and hedge-hog-like . . . " He also refers to the plants as having "exceedingly glutinous sheaths." This feature is absent in the herbarium specimens. Whether this is due to a change during drying (though there was no such change in the recently collected Dubbo plant) or whether the remark was based on another individual plant in the locality requires checking in the field.

Distribution.—SOUTHERN QUEENSLAND: About 30 miles W. of St. George, *S. T. Blake,* No. 10786, 15.iii.1936 (BRI, CANB). NORTHERN CENTRAL NEW SOUTH WALES: Warialda, *J. L. Boorman,* Sept. 1910; Pilliga Scrub, *J. B. Cleland,* 8.x.1918; central Pilliga Forest, *G. Burrows,* No. 6, 1.xi.1917 (spikelets approaching those in var. *mitchelli*) (NSW); Narrabri, *J. L. Boorman,* Sept. 1910; also Nov. 1910 (HOLOTYPE); Warrumbungle Ranges, *W. Forsyth,* Oct. 1899 (spikelets approaching those of var. *mitchelli*) (NSW, MEL); near Dubbo, *G. Downes* and *J. Sleeman,* No. 89, 9.xi.1948 (CANB).

7. **Triodia marginata** sp. nov.

Holotype.—Cunnamulla, *K. C. Baker,* No. 865, 18.x.1949.

Affinis *T. mitchelli* sed differens ob spicula turgidiora, lemmata pallidiora, latiora, margines scariosos.

Culmi et *folii T. mitchelli* similes. *Panicula* laxa, rhachis scabra vel pubescens, paullo resinosa. *Spiculae* ovatae vel lanceolatae sed turgidae, 5-9-floriferae, 10-15 mm. longae, 6-7 mm. latae, 2-3 mm. densae. *Glumae* purpureae, post stramineae, oblongae, obtusae, rigidae, cartilagineae vel induratae, subaequales, 5-7 mm. longae, 3-3.5 mm. latae. *Lemmata* late ovata, pallida, ad basim pubescentia, supra medium glabra, trilobata; lobi laterales acuti, ciliolati, trinervati, lobi medii concavi; margines lemmatium et loborum lateralium alati, scariosi. *Paleae* ellipticae, 4-6 mm. longae, carinis alatis, alis ciliolatis; apices angusti, truncati, pubescentes, 0.5 mm. longae vel minores.

The plants are similar to those of *T. mitchelli* var. *mitchelli* and form tussocks about half a metre in diameter or larger, and in older plants the centre dies away, leaving a ring or crescent. Leaves as in *T. pungens* and *T. mitchelli* var. *mitchelli*. *Panicles* standing about 1 m. high in the tussocks, the lateral branches slender and with 3-6 spikelets on the lower ones, rhachis scabrid to scabrid-pubescent, slightly resinous. *Spikelets* on capillary pedicels, 5-11-flowered, broadly ovate to lanceolate or linear-lanceolate when many-flowered but thicker and more turgid than those of *T. mitchelli* var. *mitchelli*, 10-16 mm. long, 6-7 mm. wide, and 2-3 mm. thick. *Glumes* purplish though paler than those of *T. mitchelli* var. *mitchelli* and fading to straw-coloured with age, with 3 main nerves and with 1 or 2 pairs of lesser nerves in the upper half, very stiffly scarious or hardened and indurate. *Lemmas* broadly ovate, pale except for a slight colouring of the tips of the lobes, 4.5-7 mm. long and almost as wide, entire portion with soft white hairs covering at least half the length, upper part below the lobes and the lobes glabrous; lobes about a quarter as long as the total length, broad, acute, ciliolate, each with 3 nerves which are obscure in the entire portion and with an additional pair entering the base of the middle lobe. Margin of the lateral lobes with a scarious edge curving in a wide arc to the base of the lemma and conspicuous in the spikelet. In the other members of the *T. mitchelli* complex there is sometimes a scarious edge in the upper part but it is never as wide nor does it extend to the base as in *T. marginata*. *Paleas* with very narrow ciliolate wings on the nerves, the apices with short, narrow, pubescent tips barely 0.5 mm. long fitting into the concavity of the median lobe of the corresponding lemma but, in some specimens, slightly recurved (probably after anthesis) (Fig. 8(*c*) *C-H*).

While there seems little doubt that this is a member of the *T. mitchelli* complex, no intermediate variations have been seen and it therefore appears to be distinct.

Distribution.—SOUTH-WEST QUEENSLAND: Charleville, *S. T. Blake*, No. 5410, 20.iv.1934 (BRI, CANB) also *C. T. White*, No. 11678, 16.xii.1941; Yarmouth, S. of Wyandra, *L. J. Walker*, Nov. 1936; near Cunnamulla, *C. T. White*, No. 11583, 3.iv.1941 (BRI); Gilruth Plains, Cunnamulla, *J. G. Davies*, May 1933; also *M. J. Mackerras*, Nov. 1939; also *K. H. L. Key*, Oct. 1940; also *R. Roe*, No. 358, 22.vii.1941; also *A. Callander*, Jan. 1949; also *K. C. Baker*, Nos. 864 and 865 (HOLOTYPE), 18.x.1949 (CANB); Bollon-Cunnamulla Rd., *R. Roe*, No. 17, Oct. 1938 (BRI); Nindigully district, *R. Roe*, Nov. 1938; Yuleba, *R. Soutter*, Oct. 1943 (BRI).

8. **Triodia basedowii** Pritzel in Fedde Repert. 15: 356 (1918).

Syntypes.—Central Australia, *H. Basedow* 1903. Elder Exploring Expedition, Arkaringa Creek. It is possible that Basedow's Nos. 315 and 425 may represent *haptotype* material.

The original description of this species is not readily available in Australia and is therefore reprinted here.

"Rigida, ramis junioribus dense lanatis, foliis patentibus paulo curvatis pungentibus subteretibus. Inflorescentia subspicata densa, ramulis erectis brevibus. Spiculis pallidis, ca. 6-floris. Glumis inferioribus latis obtusis, glumis floriferis basi dense tomentosis, lobis 3 quam partem integrum longioribus, lobo medio paulo longiore acuminato, lobis lateralibus obtusis.

Folia 10 cm. longa vel longiora. Inflorescentia 6-8 cm. longa, 1-1.5 cm. lata. Spicula 8-9 mm. longae, apertae ca. 5 mm. latae. Glumae inferiores ca. 6 mm. longae, 2 mm. latae, glumae floriferae ca. 6 mm. longae.

Species ex affinitate *T. pungentis* R. Br. sed ramis lanatis, glumis floriferis profundius trilobis, obtusioribus, spiculis majoribus diversa.

Hab. in Australiae centrali (districtu C sec cl. Tate) leg. H. Basedow, 1903. Ab expeditione Elderiana ad "Arkaringa Creek" in Australia australi collecta et cl. F.v. Mueller et Tate *T. pungens* nominata specimena in herbaris Kewense adsunt."

The above description can be amplified, on the basis of other specimens, as follows: tussocks pyramidal and sometimes becoming annular or crescentic owing to the death of the older culms in the centre. *Leaf sheaths* woolly-tomentose, especially around the orifice though the lower parts of the sheaths and the sheaths of older leaves may become more or less glabrous. *Spikelets* pedicellate on short branches of the panicle, the lemmas usually spreading towards the apex giving a cuneate and truncate outline. *Glumes* many-nerved and rounded on back, broad-lanceolate to oblong, obtuse or acute, 6-8 mm. long, 2-4 mm. wide. *Lemmas* with a horny-indurate and pubescent base shorter than the stiffly scarious lobes, which are ciliate and rarely sparsely hairy. The median lobe acuminate, the laterals obtuse or acute, all with 3-5 nerves (rarely 7) rendered conspicuous by the associated chlorenchyma, the rest of the lobe reddish purple or pallid when old. *Paleas* oblong or obovate, the nerves scabrid, the texture membranous but slightly thicker below than at the ragged apex, which is curved over the floral organs.

Distribution.—Central Western Australia to western Queensland. The following localities are additional to those previously published (Burbidge 1946*a*). WESTERN AUSTRALIA: Wiluna, *G. F. Melville,* July 1937 (MEL). CENTRAL AUSTRALIA: Government North West Expedition, *Dr. H. Basedow,* Nos. 315 and 425, 1903 (HAPTOTYPES?) (NSW); Elder Exploring Expedition, camp 6, *R. Helms,* 21.vi.1891 (NSW, MEL, AD); 110 miles SW. of Lake Nash Station, *R. A. Perry,* Nos. 900 and 901, 22.v.1948 (CANB); Simpson Desert Expedition, 2 miles W. of camp 8, between sandhills, *R. L. Crocker,* 13.vi.1939 (BRI, AD); base of sandhills E. of Andado Station, Simpson Desert Expedition, *R. L. Crocker,* 29.v.1939; between sand ridges 2 miles N. of Mayfield Swamp, Andado Station, *R. L. Crocker,* 2.vi.1939 (AD); 10 miles S. of Anacoora Bore, *G. H. Clarke* (ADW); sandhills near Farina, S.A., *Mrs. J. Stanford* (AD); Central Australia, *S. Newland,* Nos. 137, 138, and 141, June 1887 (MEL). QUEENSLAND: Mulligan River, *H. Clarke,* Feb. 1904 (NSW); Frazerborough,

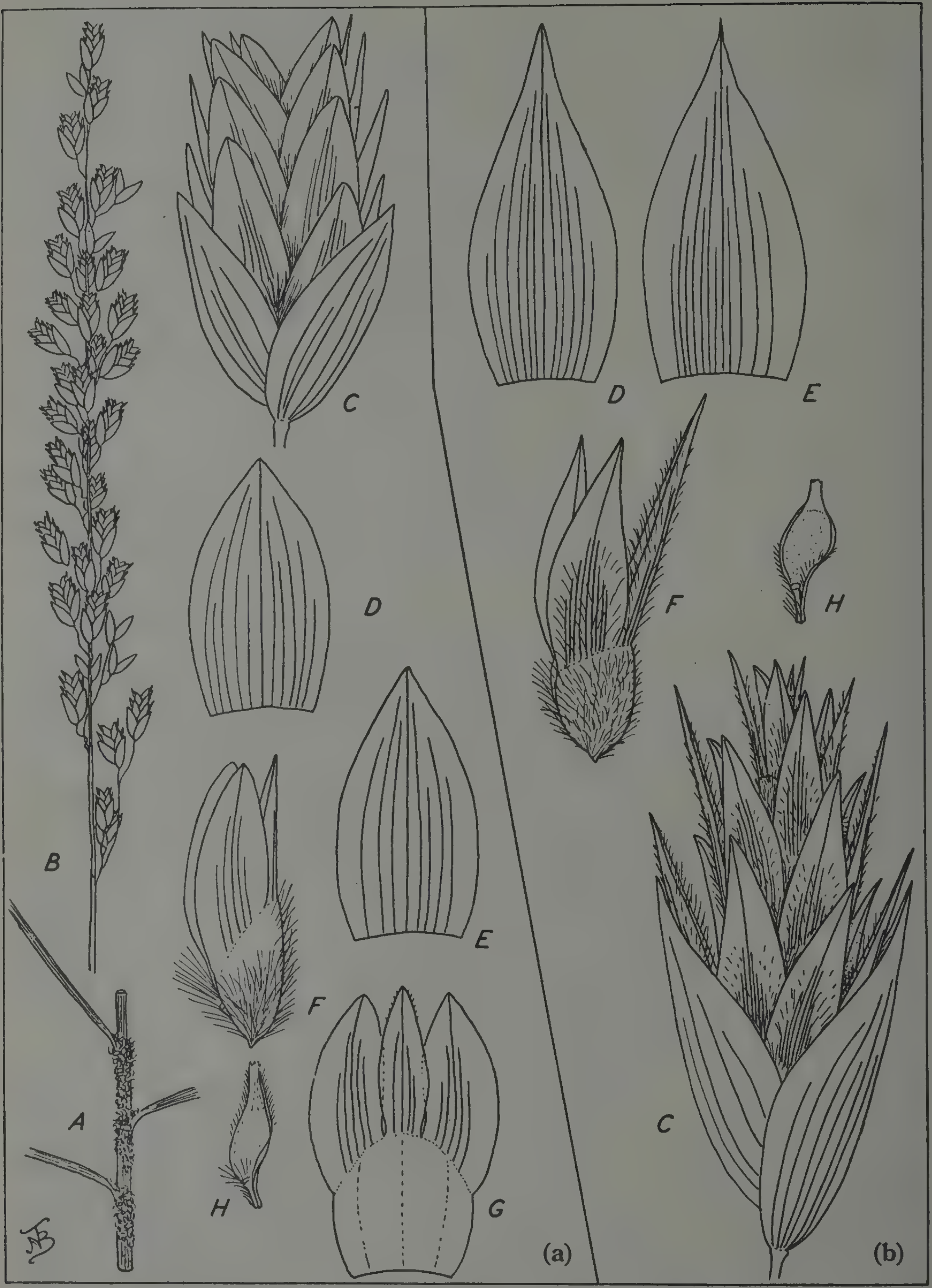
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Fig. 9.—(*a*) *Triodia basedowii* Pritzel, from *Crocker*, 13.vi.1939. (*b*) *T. lanigera* Domin, from *Burbidge*, No. 454. Lettering as in previous figures.

Jundah, *E. M. Bowman,* No. 3, 1938 (BRI); Tenham Station, 25° 50′ S. 142° 50′ E., *S. T. Blake,* No. 12035, 9.xi.1936; Windorah sandhills, *S. T. Blake,* No. 12097, 13.vii.1936; near Windorah on low sandhills, *S. T. Blake,* No. 12061, 10.vii.1936 (BRI, CANB); 30 miles S. of Bedourie, *S. T. Blake,* No. 12286, 21.vii.1936 (BRI), 83 miles N. of Tibooburra, N.S.W., *E. F. Riek and I. Common,* No. 0209, 3.xi.1949 (CANB).

9. **Triodia lanigera** Domin in J. Linn. Soc. (Bot.) 41: 278 (1912).

Holotype.—Between Ashburton and Yule Rivers, *Dr. E. Clement.*

This species is confined to Western Australia and appears to be extremely closely related to *T. basedowii* from which it differs in the longer acuminate lobes of the lemmas, the pubescence of the lobes, the indurate base of the paleas, and the acute-acuminate or slightly aristulate glumes.

Tussocks usually hemispherical or pyramidal. *Culms* woolly at and below the nodes or, on unbranched portions, glabrous or glabrescent. *Leaf sheaths* tomentose with woolly hairs, becoming glabrescent with age but more tomentose than in *T. basedowii.* Orifice with woolly hairs. *Laminae* minutely but evenly striate under a lens, appearing terete (actually conduplicate), pungent-pointed. *Panicles* open, about the same size as in *T. basedowii,* rhachis scabrid with tufts of woolly hairs at the bases of the branches, which bear 4-6 spikelets. *Spikelets* pedicellate, cuneate. *Glumes* lanceolate or oblong, acute, acuminate or aristulate, 9-13-nerved, 8-12 mm. long, 4-4.5 mm. wide, margins minutely ciliolate. *Lemmas* with a horny-indurate, softly pubescent base which, in the lowest lemma, is 2-3 mm. long, and 3 stiffly scarious lobes each with 3-5 nerves (rarely 7); lobes acuminate, ciliolate, softly pubescent, especially towards the base, median lobe 7-10 mm. long and the laterals 4-6 mm. *Paleas* obovate or oblong, the base hardened, the upper part membranous, 3-4 mm. long in the lowest lemma, the nerves ciliate.

Distribution.—Western Australia: Gascoyne, King (NSW); between Gascoyne and Fortescue Rivers, *H. S. King,* 1885 (MEL) (for other localities see Burbidge 1946*a*).

10. **Triodia plectrachnoides** sp. nov.

Holotype.—Cannon Hill, about 12° 24′ S., 132° 55′ E., *S. T. Blake,* No. 17132, 2.ix.1946.

Affinis *T. roscidae* N. T. Burbidge sed laminis glabrioribus, paniculis laxioribus, spiculis magis pedicellatis, lobis lemmatium inaequalibus.

Culmi glabri. *Foliorum vaginae* glabrae. Orificia barbata, villi breves, erecti, 1 mm. longi. *Laminae* glabrae. *Panicula* laxa, 20 mm. longa, rami graciles, laeves vel scabriduli. *Spiculae* oblongae, pedicellatae; pedicelli leviter filiformes, ad 2.5 cm. longae; 2-4-floriferae. *Glumae* oblongae, scabridulae, acutae, vel obtusae, aristulatae, induratae, 3-nervis; medio nervo prominente, scabro. *Lemmata* oblonga, trilobata; lobi aristulati, inaequaliter, medio lobo longiore; infima ad 7 mm. longa. (lobis incluis), infra medium pubescentia. *Paleae* membranaceae, carinis ciliolatis, 2 mm. longae.

Except for the orifices the leaves are smooth and quite glabrous. The top of the sheath is asymmetrical and slightly auriculate on one side, the small auricles being thinner in texture and brownish. The hairs of the orifice are erect, soft but shining, and longer than the similar hairs of the ligule. *Panicles* open and more lax than in any other species, the lateral branches being very slender and the filiform pedicels of the spikelets longer than in other species. *Spikelets* oblong, characterized by the aristulate glumes and the slender awns of the lemma. *Glumes* with a scabrid central nerve, which extends as a short awn above the acute, obtuse, or slightly lobed apex. On the type specimen the glumes have occasional minute patches or droplets of secretion similar to those in *T. roscida*. *Lemmas* appear empty in the type and may not be fully developed. The basal part is thinner in texture but there is a nerve, extending to each lobe, with vestigials in the lower part; the entire portion is pubescent along the margin and in the lower part of the median line but the upper part is glabrous below the subulate lobes. The lateral lobes are flatter than the awn-like median one, which is twice as long (i.e. 2-3 mm.). *Paleas* more than half as long as their lemmas but possibly not fully developed, nerves ciliolate but not winged. Fine tufts of hairs on the joints of the rhachilla below the lemma obscure the minute callus (Fig. 11(*b*) *A-H*).

Some hesitation was felt before attempting to base a new species on the extremely poor specimen, the only one available. However, the open panicle with its long-pedicelled spikelets and the unequal and awn-like lobes of the lemma make it quite distinct. There being therefore no doubt as to its special character and having studied such a large volume of *Triodia* material during the preparation of this paper the writer felt that for completeness at least, this new species should be included. It is close to *T. roscida* in that there are indications that similar secretions are developed, but it is also related to *T. burkensis*, differing in the length of the pedicels, the aristulate glumes, and the unequal aristulate lobes of the lemmas, which resemble those in *T. stenostachya* although so much larger. The hairs of the orifice resemble those in *T. wiseana* and *T. intermedia*.

The name was chosen because of the lobes of the lemma but apart from this it is quite distinctly a *Triodia*, the relatively short oblong and boat-shaped glumes being quite unlike the long lanceolate structures found in *Plectrachne*, and the lobes of the lemma are shorter in proportion to the entire part.

Distribution.—Cannon Hill, about 12° 24′ S., 132° 55′ E., on exposed rocky slopes, *S. T. Blake*, No. 17132, 2.ix.1946. "Greenish, branched tussocks; culms up to 3 metres" (HOLOTYPE) (CANB, BRI).

11. **Triodia wiseana** var. **wiseana** (C. A. Gardner sens. orig.) comb. et. stat. nov. *T. wiseana* C. A. Gardner in J. Roy. Soc. W. Aust. 27: 166 (1942).

Holotype.—Mount Margaret Pass, Hamersley Range, *C. A. Gardner*, No. 3129.

Culms glabrous. *Leaf sheaths* glabrous or (in northern specimens) sometimes hirsute towards the top with hairs similar to those at the orifice. Orifices with conspicuous, erect and shining hairs 3-5 mm. long which continue along the lower part of the margins of the laminae where they may arise in groups from small swellings. *Laminae* rigid, divaricate, pungent pointed, with a line of translucent glands sometimes visible along each ridge of the striations. *Panicle* 6-20 cm. long, loose, rhachis scabrid. *Spikelets* compact, oblong to linear-lanceolate, 8-12 mm. long, 5-9-flowered, shortly pedicellate. *Glumes* lanceolate to oblong, acute, acuminate, or mucronate and rather obtuse, indurate but not very stiffly so, glabrous to scabridulous, about equal in length, 4.5-5 mm. long, 3-5-nerved; the mid nerve scabridulous or glabrous, forming a slight keel and sometimes continued above as a short mucro, the lateral nerves less distinct. *Lemmas* lanceolate to ovate-lanceolate, smoothly indurate, with 3 acuminate lobes (which may be purplish) and with a dorsal line of hairs in the lower half as well as a marginal series and a few at the base near the minute glabrous obtuse callus; nerves in 3 groups of 3 each, obscure in the base of the lemma but visible above and converging into a thickened ridge in each lobe; lowest lemma 4-6 mm. long. *Paleas* slightly longer than the entire part of the corresponding lemma but not as long as the lobes, glabrous; the nerves winged and the wings sometimes protruding in the spikelet (Fig. 10(*a*) *A-H*).

This species was formerly known only from the north-west of Western Australia but specimens have been collected in Central Australia and in the Kimberley district. Cleland's specimen from Mount Liebig is not typical as it has scarious glumes as long as the spikelet.

Distribution.—WESTERN AUSTRALIA: between Port Hedland and Abydos Station, *C. M. Donald,* Oct. 1946; 20 miles S. of Lissadell Station, Kimberley, *R. A. Perry,* No. 2676, 3.viii.1949; 12.5 miles S. of Turner Station, *R. A. Perry,* No. 2412, 11.vii.1949; 16 miles N. of Nicholson Station, *R. A. Perry,* No. 2377, 19.vi.1949. NORTHERN TERRITORY: 45 miles SW. of Victoria Downs Station, *R. A. Perry,* No. 2177, 19.vi.1949; near Wave Hill Police Station, *R. A. Perry,* No. 2251, 26.vi.1949. CENTRAL AUSTRALIA: top of Mount Liebig, *J. B. Cleland,* No. L32, 14.viii.1932 (CANB) (cf. Burbidge 1946*a*, p. 24).

11a. **Triodia wiseana** var. **brevifolia** N. T. Burbidge in J. Roy. Soc. W. Aust. 30: 24 (1946).

Holotype.—Nullagine Rd. S. of Mount Edgar Station, *N. T. Burbidge,* No. 1152.

This variety differs from *T. wiseana* var. *wiseana* in that the hairs of the orifice do not extend along the margins of the laminae, which are shorter and more slender (Fig. 10(*a*) *A′*). In the field when the plants are fresh the hairs of the orifice and on the base of the petiole-like portion tend to lie against the margins so that they are not at all conspicuous. The spikelets are similar to those in *T. wiseana* var. *wiseana* except that the lemmas are a little more deeply lobed and the lobes are slightly spread and closer in resemblance to those in *T. pungens.*

Distribution.—WESTERN AUSTRALIA: between the 80-Mile Beach and the Ashburton River (Burbidge 1946).

12. **Triodia intermedia** Cheel in K. svenska VetenskAkad. Handl. 52(10): 4-5 (1916).

Holotype.—Noonkanbah, West Kimberley, Mjoberg's Swedish Sci. Exped., Dec. 1910 (No. 18).

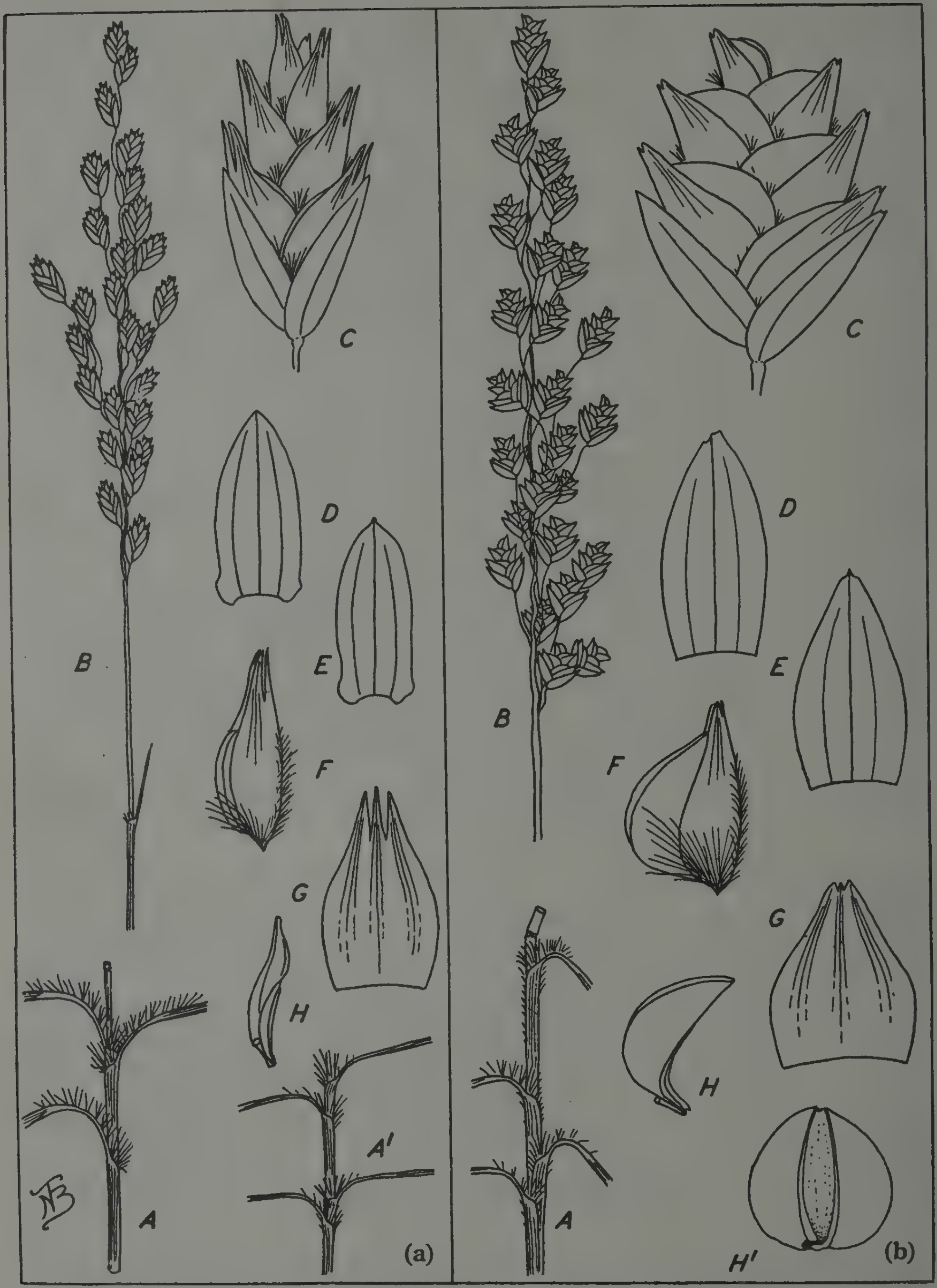
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Fig. 10.—(*a*) *Triodia wiseana* var. *wiseana*, from *Donald*, Oct. 1946 (A′ represents portion of a culm from var. *brevifolia* N. T. Burbidge). (*b*) *T. intermedia* Cheel, from *Perry*, No. 2493. Lettering as in previous figures.

Culms glabrous. *Leaf sheaths* with shining flaccid hairs 3-4 mm. long at the orifices and extending down along the margins of the sheaths and up on to the margins and adaxial surfaces of the petiole-like bases of the laminae. Ligule scarious-ciliate or ciliate. *Laminae* 8-20 cm. long, pungent pointed, glabrous except at the base and with a single row of translucent glands often discernible along each ridge of the striations, the glands sometimes slightly raised above the general surface level. *Panicle* loose but narrow, rhachis scabrid. *Spikelets* oblong to cuneate with the upper florets divergent, pedicellate, 6-10-flowered, 8-10 mm. long, 4-6 mm. wide. *Glumes* broadly lanceolate or oblong, acute, slightly mucronate or ragged at the apex, approximately equal, 4-6 mm. long, glabrous, stiff, and often shining, pale or faintly purplish, 3-nerved (rarely 5-nerved), the mid nerve forming a slight keel, the laterals less conspicuous. *Lemmas* ovate and narrowed into the tridentate apex, often purplish except when old, lowest 3-5 mm. long, 2.5-4 mm. wide; with shining hairs at base, on the lower part of the median line and on the lower margins, glabrous above; lobes ciliolate. Callus minute, obtuse, glabrous below. In the spikelet the lemmas often appear as broad as long owing to the conspicuously protruding wings on the nerves of the palea. *Paleas* glabrous, almost as long as their lemmas, the apices obtuse and the nerves with wings 1-1.5 mm. broad, which are very conspicuous and often purplish like the lemmas (Fig. 10(*b*) *A-H′*).

In the study of the Western Australian species (Burbidge 1946*a*) the opinion was expressed that this species did not belong in *Triodia*. At the time no specimens were available and the remark was based on a drawing of a spikelet and floret which appeared quite unlike anything then known to the author. However, in 1948 a specimen was obtained by Mr. E. C. B. Langfield at Fitzroy Crossing, to the east of the type locality of *T. intermedia* on Noonkanbah Station. This material seemed to agree closely with *T. intermedia* and there is no doubt of its generic position. Further material was obtained in the Kimberleys and Northern Territory by Mr. R. A. Perry during the 1949 trip of the Northern Australian Regional Survey party.

The description given above was based on these recent collections, which do not agree in all details with Cheel's diagnosis. For example, he described the leaves as "glabrous, shiny or the short sheath sparingly sprinkled with hairs along the margin and upper part of the sheath; ligule very short, scarious." In our material the orifices have copious hairs similar to those in *T. wiseana* but softer, while the ligule is scarious-ciliate on some of the lower leaves but merely ciliate above. His description of the lemma as "3-nerved with a set of three nerves between the main nerves" is confusing while "palea . . . . slightly larger than the flowering glumes" makes no reference to the very conspicuous wings on the nerves. However, the "flowering glume entire or minutely lobed" would fit no other species known from the area, especially when the size of the panicle and its spikelets is taken into account.

Distribution.—WESTERN AUSTRALIA: Fitzroy Crossing, *E. C. B. Langfield*, 1948; 15 miles E. of Flora Valley Station, Upper Ord River, *R. A. Perry*, No. 2493, 15.vii.1949. NORTHERN TERRITORY: 13 miles SW. of Wave Hill Station, *R. A. Perry*, No. 2203, 21.vi.1949 (CANB).

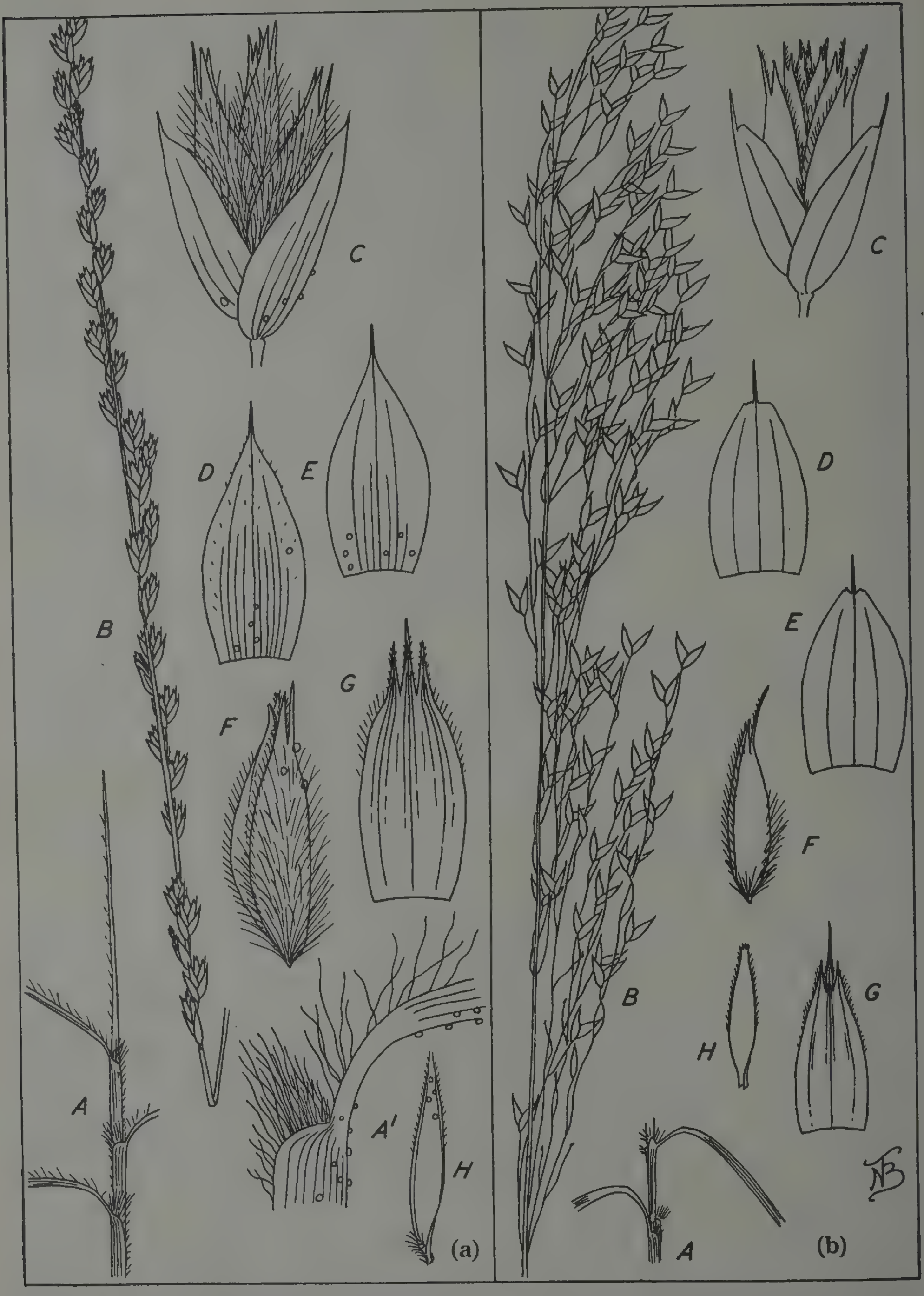
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Fig. 11.—(*a*) *Triodia roscida* sp. nov., from *Perry*, No. 2404. (*b*) *T. plectrachnoides* sp. nov., from *Blake*, No. 17132. Lettering as in previous figures.

The Fitzroy Crossing material was growing on sandy loam but Perry's specimens were found on stony ground or on rocky slopes. He describes the tussocks as about 2 ft. in diameter and 1 ft. high.

13. **Triodia brizoides** N. T. Burbidge in J. Roy. Soc. W. Aust. **30**: 24 (1946).

Holotype.—Gorge Range, between Shaw and Coongan Rivers, *N. T. Burbidge,* No. 792.

Forming dense hemispherical tussocks 20-30 cm. high (see Burbidge 1945, Plate xxii, Fig. 3). *Culms* slender but rigid, glabrous. *Leaf sheaths* glabrous except for the tangled woolly but bright hairs at the orifice. These hairs extend up the adaxial surface of the petiole-like bases of the laminae. *Laminae* conduplicate, appearing terete, glaucous, minutely but evenly striate, slender, pungent pointed. *Panicles* diffuse and with few spikelets on filiform pedicles up to 20 mm. long attached to the main rhachis or to capillary lateral branches; rhachis and pedicels scabrid, small tufts of hairs being present at the bases of pedicels and of lateral branches. *Spikelets* 7-10-flowered, 10-20 mm. long, 6-8 mm. wide, oblong in outline and laterally flattened. *Glumes* oblong, acute or obtuse, aristulate or mucronate, equal or subequal, glabrous, stiffly scarious, 3-5-nerved, 6-6.5 mm. long. *Lemmas* lanceolate or ovate, with 3 groups of 3 nerves, which are more evident above; lowest lemma 5-7 mm. long, pubescent at the base and bearded on the margin, shortly 3-lobed, the lobes narrow, acute-acuminate, and subequal. *Paleas* linear or elliptical, pubescent at the base, the nerves narrowly winged and ciliolate (Fig. 12(*a*) *A-H*).

This species has not yet been found outside Western Australia, where it grows on rocky hills to the north of Marble Bar in the Pilbara region. For details of localities see type description.

Owing to a printing error the name as originally published was incorrect. It is altered here in accordance with Art. 70 of the International Rules of Nomenclature.

14. **Triodia burkensis** sp. nov.

Holotype.—Normanton, Burke district, *S. T. Blake,* No. 9032, 20.v.1935.

Affinis *T. brizoides* N. T. Burbidge sed laminis crassioribus, spiculis minoribus, lemmatibus minoribus.

Culmi glabri vel ad nodos pubescentes. *Foliorum vaginae* glabrescentes, striatae. Orificia tomentosa; tomentum flaccidum, implicatum. *Laminae* rigidae, striatae, glabrae, pungentes. *Panicula* laxa, 7-10 cm. longa; rhachis et rami scabri. *Spiculae* ovatae vel oblongae, 4-6-floriferae, pedicellatae, pedicelli ad 10 mm. longi. *Glumae* late lanceolatae vel oblongo-lanceolatae, induratae, acutae vel acuminatae, mucronatae, subaequales, 3-5-nervis, medio nervo prominente, 4-5.5 mm. longae, supra medium marginibus ciliolatis vel glabris. *Lemmata* ovata vel lanceolata, indurata, trilobata, carinis infra medium et marginibus villosis, 9-nervis; lobi angusti, ciliolati, subaequales, 3-nervis, infima lemmata 5.5-6 mm. longa (lobis inclusis), lobi 1 mm. longi, callus minutus. *Paleae* ellipticae vel lanceolatae, glabrae, carinis alatis, alis angustissimis, ciliolatis; infimae 3.5-4 mm. longae.

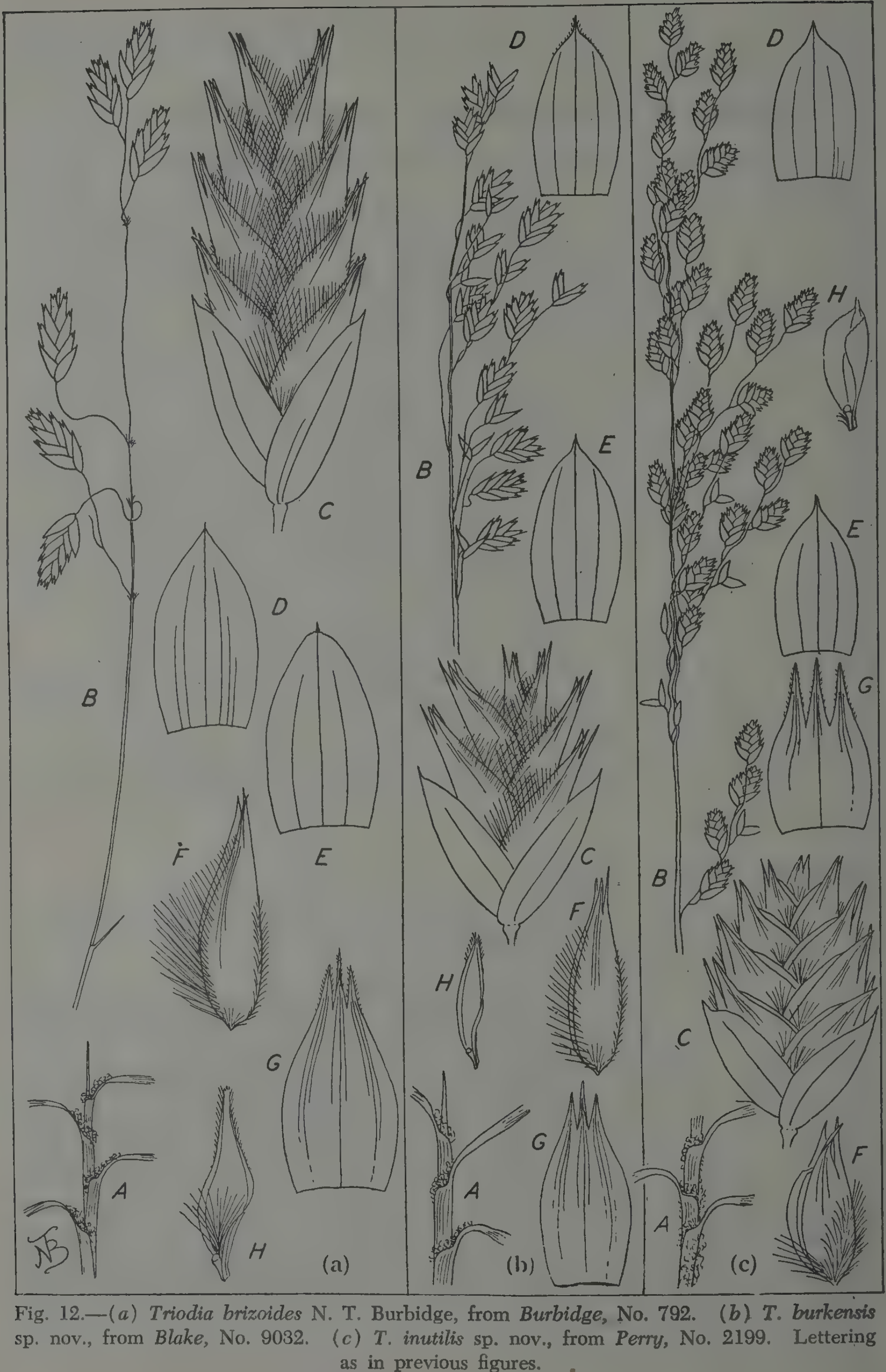
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Fig. 12.—(*a*) *Triodia brizoides* N. T. Burbidge, from *Burbidge*, No. 792. (*b*) *T. burkensis* sp. nov., from *Blake*, No. 9032. (*c*) *T. inutilis* sp. nov., from *Perry*, No. 2199. Lettering as in previous figures.

According to Blake the plants are large, very dense, irregularly shaped tussocks up to 1 m. in diameter. *Culms* either glabrous or with a patch of pubescence at the junction of the sheath with the node. *Leaf sheaths* striate and when young whitish along the striae with minute adpressed hairs visible under a lens. Orifices with flaccid but tangled hairs which continue up the adaxial surface of the petiole-like base of the laminae. *Laminae* glabrous and smooth to the touch though striate under a lens, very rigid, and pungent pointed. *Panicles* loose though in dried material they are narrow owing to the erect position of the branches, rhachis and also the branches and pedicels scabrid. *Spikelets* more or less oblong owing to the divaricate lemmas. Possibly in younger specimens these would be more closely distichous. *Lemmas* hard and smooth except for the short hairs along the lower median line and the longer hairs spreading out from the submarginal areas. In the spikelet the latter hairs are quite conspicuous. Callus so minute as to be almost absent. *Paleas* in the lowest lemmas about a third as wide and almost long enough to reach the base of the lobes; nerves very narrowly winged, the wings minutely ciliolate (Fig. 12(*b*) *A-H*).

The species is only known from the Burke district in Queensland. Broadly speaking, it bears resemblance to *T. brizoides* but differs in that the hairs of the orifice are flaccid and tangled rather than woolly-tomentose and that the panicle has much more numerous spikelets which are smaller in all parts. It also approaches *T. molesta* in which the sheaths are woolly-tomentose and which has a different arrangement of hairs on the lemmas.

Distribution.—QUEENSLAND: Normanton, Burke district, on low, barren ridges with ferruginous, lateritic crust, S. *T. Blake,* No. 9032, 20.v.1935 (HOLOTYPE); Mt. Isa, Burke district, on stony ridges and plains, S. *T. Blake,* No. 8768, 24.iv.1935 (BRI, CANB).

15. **Triodia inutilis sp. nov.**

Holotype.—13 miles SW. of Wave Hill Station, *R. A. Perry,* No. 2199, 21.vi.1949.

Affinis *T. brizoides* N. T. Burbidge sed spiculis compactioribus, minoribus, paniculis longioribus, sed lemmata cum lobis magis profundis.

Foliorum vaginae ad basim lanatae vel glabrescentes; supra basim laeves vel striatae. Orificia tomentosa. Ligulae tomentosae. *Laminae* glabrae, rigidae, striatae, conduplicatae, pungentes, 10-15 cm. longae; diametros 1 mm. *Panicula* laxa, 10-15 cm. longa; rhachis angulati; anguli laeves vel scabriduli; rami scabriduli. *Spiculae* 7-9-floriferae, pedicellatae, ovatae vel oblongae, obtusae, stramineae, 7-9 mm. longae, 3.5-5 mm. latae. *Glumae* oblongae, rigidae, scariosae vel induratae, subaequales, 4-5 mm. longae, acutae vel apiculatae, 3-nervis (raro 5-7-nervis), glabrae sed nervo medio scabro. *Lemmata* indurata, trilobata; lobi rigidi, erecti, subaequales, apices subulati, acuminati, margines ciliolati; infima lemmata 5 mm. longa, dorsa infra mediam partem villosa; item margines prope basim; callus minutus. *Paleae* membranaceae, glabrae, ellipticae; infimae 4-4.5 mm. longae, nervis alatis, alae 0.5-1 mm. latae.

Forming rigidly branched tussocks about 30 cm. high with flowering culms to 60 cm. (Blake). *Culms* branching in the usual manner, pubescent at the nodes and just below, longer internodes glabrescent in the lower portion. *Leaf sheaths* rounded on the back, woolly-pubescent towards the base and along the margins but sometimes glabrescent, stiff, smooth or minutely striate. Orifice and ligule with dense tomentose hairs, which extend up the adaxial surface of the petiole-like base of the lamina. *Laminae* rigid and pungent pointed, minutely striate under a lens. *Panicle* loose, the rhachis slightly hollowed behind the capillary lateral branches, the angles thus formed being smooth or scabridulous. Lateral branches and pedicels of the spikelets scabridulous. *Spikelets* ovate or oblong in outline and often rather more flattened than in other species, obtuse, straw-coloured or the lobes faintly purplish. *Glumes* oblong or lanceolate with a narrow pointed apex, stiff or hardened, especially towards the base, glabrous, with a scabrid median nerve and 1 lateral nerve on either side (rarely another lesser nerve). *Lemmas* 7-9; deeply 3-lobed (to about half total length); lobes stiff, erect or slightly spreading, subequal, flat at base to subulate at the narrow-acuminate points, margins smooth or minutely ciliolate; entire portion indurate and of the same general texture as the lobes, with a strip of soft hairs up the median line almost to the base of the mid lobe and another group of hairs on the lower third of the margins, the rest glabrous except for a very short hairy callus. *Palea* glabrous, texture between the nerves very thin, with a narrow membranous tip fitting into the concavity of the mid lobe of the lemma or sometimes ragged at the apex; nerves winged, the wings 0.5-1 mm. wide and often visible in the spikelet but not distorting the appearance of the floret as in *T. intermedia* (Fig. 12(*c*) *A-H*).

Distribution.—NORTHERN TERRITORY: 6.5 miles S. of Limbunya Station (80 miles W. of Wave Hill), *R. A. Perry*, No. 2336, 4.vii.1949; 50 miles W. of Wave Hill Police Station, *R. A. Perry*, No. 2301, 28.vi.1949; 20 miles W. of Wave Hill Police Station, *R. A. Perry*, No. 2258, 27.vi.1949; 13 miles SW. of Wave Hill Station, *R. A. Perry*, No. 2199, 21.vi.1949 (HOLOTYPE); 28 miles E. of Newcastle Waters, *R. A. Perry*, No. 351, 13.vii.1947; 8 miles N. of Helen Springs Station, *R. A. Perry*, No. 137, 29.vi.1947; 5 miles E. of Helen Springs Station, *R. A. Perry*, No. 198, 5.vii.1947; 10 miles S. of Gingera Bore, Helen Springs Station, *R. A. Perry*, No. 1909, 15.viii.1948; near October Creek, 16° 31′ S., 135° 1′ E., *S. T. Blake*, No. 17641, 4.v.1947; Three Nobs, 16° 31′ S., 135° 30′ E., *S. T. Blake*, No. 17753, 13.v.1947 (CANB).

16. **Triodia molesta** sp. nov.

Holotype.—Selwyn, S. T. Blake, No. 6400, 25.v.1934.

Affinis *T. longicepti* J. M. Black sed vaginis tomentosioribus, spiculis lanceolatioribus, glumis 5-7-nervatis, sed lemmata cum lobis magis profundis.

Culmi puberuli vel glabrescentes, ad nodo villosi sed nodi superiores glabri. *Foliorum vaginae* tomentosae. Orificia tomentosa; tomentum lanatum. *Laminae* rigidae glabrae (petiolis exclusis), pungentes. *Panicula* angusta, 10-30 cm. longa; rhachis et rami scabri. *Spiculae* lanceolate, 10-14 mm. longae, 3-4.5 mm. latae, pedicellatae; pedicelli 1-5 mm. longi. *Glumae* lanceolatae vel oblongae, induratae sed in marginibus scariosae, acutae, mucronatae, subaequales, 4.5-6

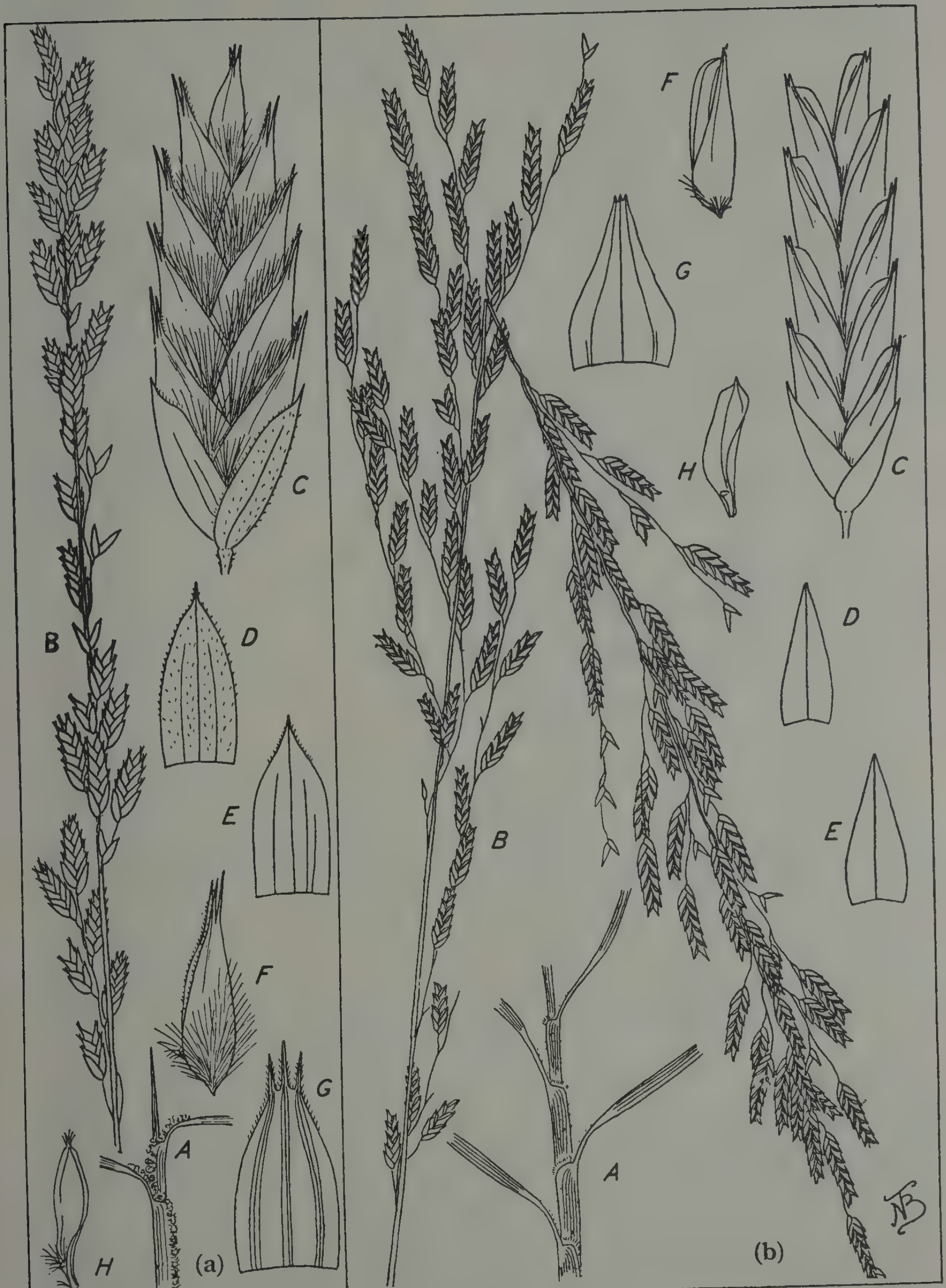
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Fig. 13.—(*a*) *Triodia molesta* sp. nov., from *Blake*, No. 6400. (*b*) *T. longiceps* J. M. Black, from *Stewart*, 3.iv.1941. Lettering as in previous figures.

mm. longae, 5-7-nervis, medio nervo supra mediam partem prominente. *Lemmata* ovata vel lanceolata, indurata, trilobata, ad basim villosa; carina infra mediam partem villosa; lobi angusti, ciliolati, subaequales, ad 1 mm. longi; infima lemmata 5.5-6 mm. longa. *Paleae* ellipticae, glabrae, membranaceae, nervis alatis, alae integrae; infimae 4 mm. longae.

Culms minutely puberulous under a lens, the nodes villose with hairs similar to those forming the tomentum on the sheaths, orifices, and adaxial surfaces of the bases of the conduplicate laminae. *Laminae* very rigid, somewhat glaucous when fresh, thicker than those in *T. burkensis,* very pungent pointed. *Panicle* narrow with the shortly pedicellate or subsessile spikelets racemosely arranged on alternate branches (of which the lowest may be 2-3 cm. long) but not conspicuously secund. *Spikelets* lanceolate in outline and well filled but the wings of the paleal nerves never visible towards the tops of the florets as is common in *T. longiceps.* *Glumes* indurate and the median nerve more prominent than the others, especially towards the top and in the thinner apex from which it may extend as a short mucro up to 1 mm. long. *Lemmas* also indurate, bearing silky hairs on the bases and along the lower halves of the median lines, the rest of the surface smooth or very minutely scabridulous. The margins thin and ciliolate towards the top where the lemma narrows sharply into the 3 almost subulate lobes. *Paleas* about as long as the entire part of the corresponding lemmas, the nerves winged and the wings entire (Fig. 13(*a*) *A-H*).

The species can be readily separated from *T. longiceps* by the tomentose leaf sheaths, the shape of the spikelets, and the fact that the wings of the paleal nerves do not extrude in the spikelet.

Distribution.—NORTH-WEST QUEENSLAND: Burke district, Mount Isa, "chiefly on hills of ferruginous schist," *S. T. Blake,* No. 8781, 27.iv.1935 (BRI, CANB); 40 miles SSW. of Mount Isa township, *R. A. Perry,* No. 791, 9.v.1948 (CANB); Kuridala, "on shallow stony soil," *S. T. Blake,* No. 6395, 25.vi.1934; Selwyn, "on stony ground," *S. T. Blake,* No. 6400, 25.v.1934 (HOLOTYPE); Gregory North district, Tulmur Station, approx. 22° 30′ S., 142° 25′ E., *S. T. Blake,* No. 11457, 11.v.1936; Tranby Station, 22° 40′ S., 142° 25′ E., *S. T. Blake,* No. 11406, 8.v.1936 (BRI, CANB).

17. **Triodia longiceps** J. M. Black in Trans. Roy. Soc. S. Aust. **54**: 59 (1930); N. T. Burbidge in J. Roy. Soc. W. Aust. **30**: 26 (1946).

Holotype.—Finke Gorge, Hermannsberg, C. Aust., *J. B. Cleland.*

Forming large tussocks up to 2.5 m. in height and twice this in diameter. The culms are smooth and glabrous. *Leaf sheaths* glabrous or minutely puberulous, except for the very short hairs at the orifice. *Laminae* very rigid, glaucous, very pungent pointed. *Panicle* slender, with narrow linear spikelets racemose along slender lateral branches. *Spikelets* 6-21-flowered, pale greenish or tipped with purple, 8-20 mm. long, 2-3 mm. wide. *Glumes* lanceolate to ovate, keeled by the single median nerve. *Lemmas* lanceolate, indurate, glabrous or with a basal tuft of short hairs associated with the minute callus and sometimes puberulous and minutely ciliolate along the margin, 4-4.5 mm. long; 3 groups of 2 or 3 nerves obscurely visible in the lower part, the central nerve of each group extending into the corresponding small acute or obtuse lobes at the apex; mid lobe sometimes mucronate. *Paleas* slightly shorter to longer than their lemmas, the nerves winged and the wings visible in the spikelet, the apices ragged or with a narrow point fitting into the mid lobe of the lemmas (Fig. 13(*b*) *A-H*).

This species was discussed in the paper on the Western Australian material (Burbidge 1946*a*) where, owing to a misprint, the spikelets are stated to be 8-20 cm. long instead of 8-20 mm. It has a wide distribution from the west across central Australia to Queensland.

Distribution.—WESTERN AUSTRALIA: Port Hedland to Abydos Station, *C. M. Donald*, Oct. 1946; Nullagine, *T. A. L. Stewart*, 3.iv.1941 (CANB); (cf. Burbidge 1946*a* for further W.A. localities). NORTHERN TERRITORY: Hermannsburg, *J. B. Cleland*, 17.viii.1929 (HOLOTYPE) (MEL); 8 miles N. of Tennant Creek, *R. A. Perry*, No. 550, 24.iv.1948; 4.3 miles N. of Tennant Creek, *R. A. Perry*, No. 147, 30.vi.1947 (CANB); Alice Springs, *C. J. Mulhearn*, No. 67, 26.x.1947; Lake Nash Station, *S. T. Blake*, No. 17961, 29.v.1947. QUEENSLAND: 10 miles N. of Thorntonia Station, NE. of Camooweal, *R. A. Perry*, No. 1452, 12.vi.1948; 63 miles ESE. of Camooweal, *R. A. Perry*, No. 763, 7.v.1948; 4 miles SW. of Ardmore Station, E. of Urandangie, *R. A. Perry*, No. 815, 13.v.1948 (CANB); Geera, E. of Barcaldine, *S. T. Blake*, No. 10377, 6.xii.1935 (BRI, CANB); 7 miles N. of Clermont-Charters Towers Rd., *N. H. Shaw*, No. S498, 5.xi.1947 (CANB).

18. **Triodia irritans** var. **irritans** (R.Br. sens. orig.) comb. et stat. nov. *T. irritans* R.Br. in Prodr. Nov. Holl. 182 (1810); *Festuca irritans* F.Muell. Veg. Chath. Is. 59 (1864) and Fragm. viii. 129 (1874); *T. aristata* J.M.Black in Trans. Roy. Soc. S. Aust. **39**: 825 (1915).

Holotype.—South coast, *R. Brown*. The type sheet at the British Museum is labelled by Brown "Triodia irritans/ South Coast Id. 4." The number is 6258. Consultation of Brown's manuscript diary and papers reveals that the locality was on St. Peter's Isle, off Denial Bay, which was visited on February 7, 1802.

Tussocks dense. *Culms* rather shorter than in some of the related species, glabrous but concealed by the sheaths. *Leaf sheaths* glabrous, smooth or inconspicuously and minutely striate under a lens, no hairs on the outer face of the orifice, ligule visible as a dense row of cilia. *Lamina* with a petiole-like base a third as wide as the sheath, rigid, conduplicate-terete, apex slender and very pungent pointed, 8-20 cm. long, 1 mm. in diameter, grey-green, minutely but evenly striate. *Panicle* often partially enclosed by the uppermost sheath, which is looser and less indurate than the lower ones and whose lamina is much reduced (to less than 4 cm. long). *Spikelets* on slender, spreading pedicels 0.5-1.5 cm. long; almost cuneate in outline owing to the long, divergent glumes, 1.5-2 cm. long, 5-10-flowered. *Glumes* as long or almost as long as spikelet, always longer than the lowest lemma, 1-2 cm. long, lanceolate, acuminate, equal or almost so; 5-nerved, the outer pair of nerves short and sometimes absent; slightly keeled, glabrous. *Lemmas* lanceolate, scabridulous, with silky hairs on the callus and the joints of the rhachilla similar to those on the base and median line of lemmas; lateral lobes up to 1 mm. long, acute or obtuse, enervate; lateral nerves in the 3 groups short and poorly developed, the longer ones not central to the lateral lobes but the mid nerve continued as a short awn equal to or longer than the lateral lobes (up to 2 mm. longer); lowest lemma 6-12 mm.

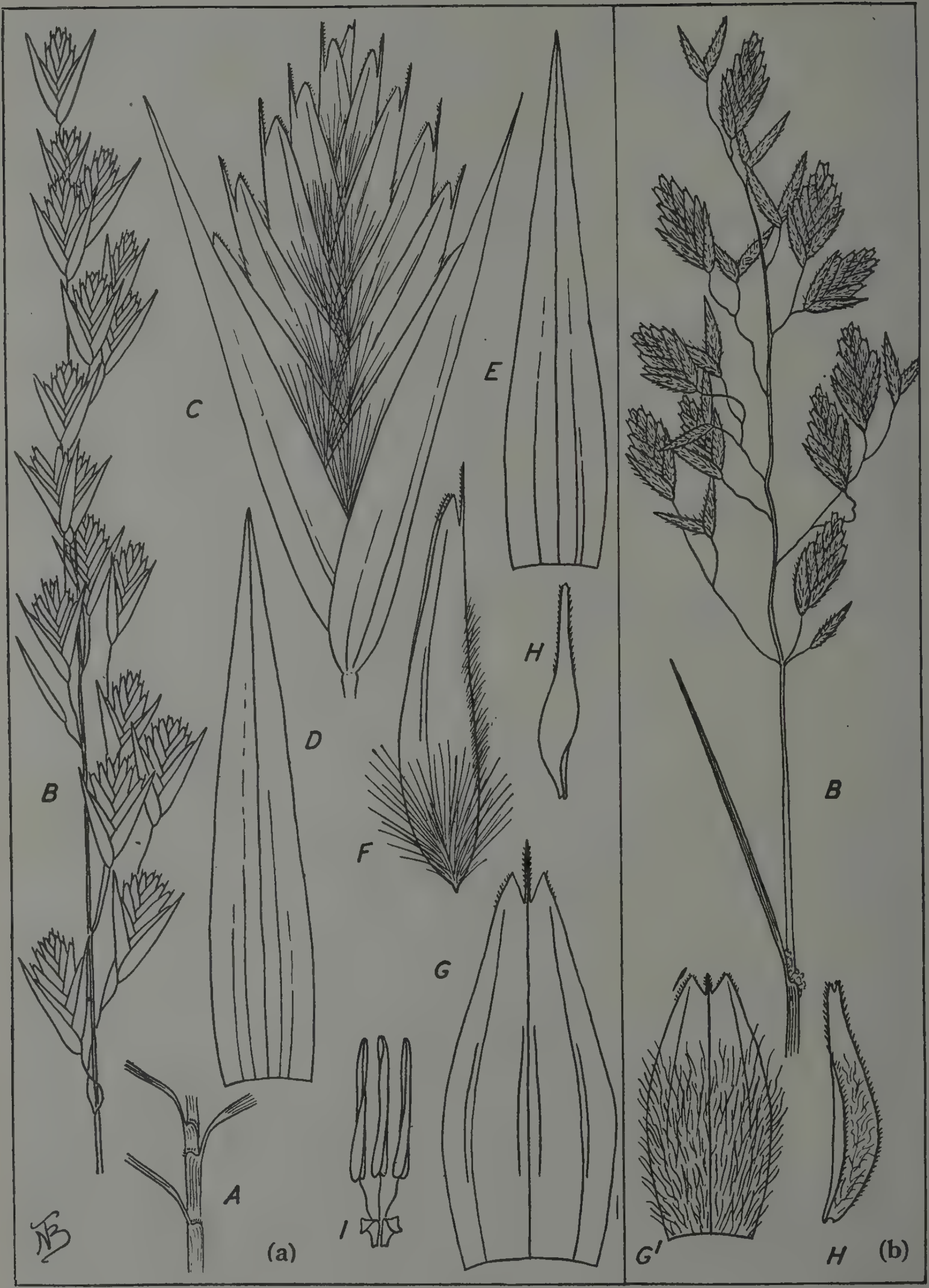


Fig. 14.—(*a*) *Triodia irritans* var. *irritans*, from *Cleland*, Ernabella, Aug. 1933. (*b*) *T. lanata* J. M. Black (after J. M. Black (1916), Plate 5). In this *G′* = abaxial surface of lemma. Lettering as in previous figures.

long. *Paleas* linear or elliptical, with the 2 nerves thickened towards the base and ciliolate above, 3.5-6 mm. long, glabrous on back. *Anthers* 3, 3-4 mm. long, purplish or brownish (Fig. 14(*a*) *A-I*).

Following Bentham (1878) most authors, including the writer, have applied Brown's name to forms in which the central lobe of the lemma is extremely short or quite absent so that the apex appears retuse or semitruncate. However, Brown's original specimen agrees with type material of *T. aristata* J. M. Black (held at Kew) better than it does with other coastal specimens such as those listed under the next variety. The spikelets are mostly empty but the glumes are long, acuminate, and comparatively thin, while the remaining lemmas have a distinctly aristate central lobe.

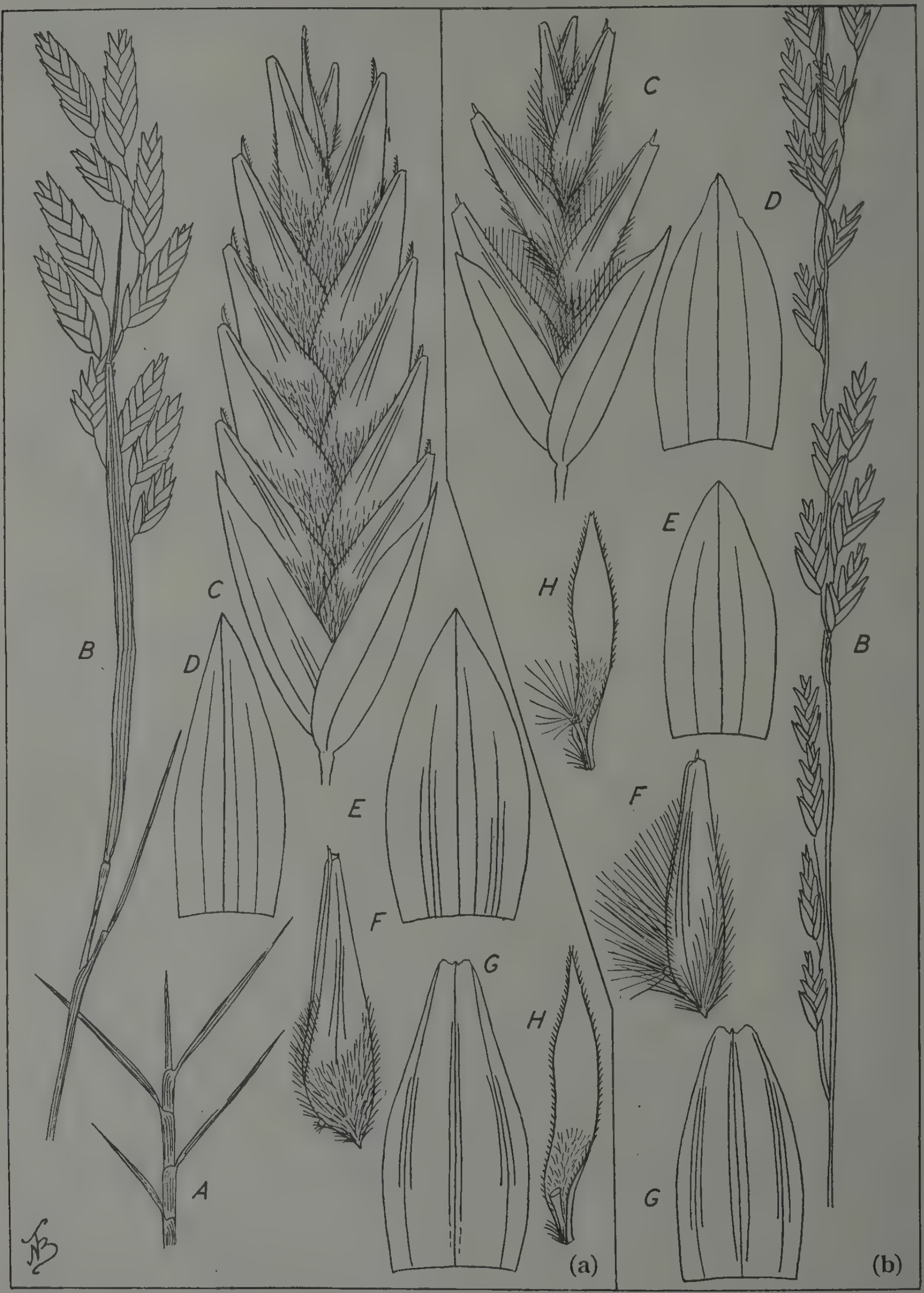
Distribution.—CENTRAL AUSTRALIA: Gosse's Range, E. Giles 1872 (not typical) (MEL); Mt. Connor, *J. M. Bechervaise,* 5.ix.1947 (MEL). SOUTH AUSTRALIA: half way between Moorilyana and Ernabella, Musgrave Range, "forming tussocks on the mountains and their bases," *J. B. Cleland,* 7.viii.1933; Ernabella, *J. B. Cleland,* Aug. 1933 (BRI); Everard Range, S. A. *White,* 2.viii.1914 (MEL); Mount Lyndhurst, *Max Koch,* No. 770, Apr. 1900 (NSW, AD); Gawler Range, *R. L. Crocker,* 21.x.1938; Elbow Hill, Eyre Peninsula, *R. L. Crocker,* Sept. 1944 (ADW) also 12.x.1944 (CANB); Wirulla, Eyre Peninsula, *Richardson,* Mar. 1931 (ADW); Mount Livington, *W. Langley,* Nos. 243 and 244, Aug. 1897 (NSW).

19. **Triodia irritans var. compacta var. nov.**

Holotype.—Elliston Beach, Eyre Peninsula, *J. H. Willis,* 26.viii.1947.

Affinis *T. irritanti* R.Br. sed spiculis compactioribus, glumis et lemmatibus induratis, 8-12-floriferis.

Culms glabrous, forming dense tussocks which may be low and spreading in exposed coastal habitats. *Leaf sheaths* glabrous, indurate, minutely striate or almost smooth. The orifice almost glabrous but the short hairs of the ligule visible. *Laminae* very rigid, glabrous and sometimes slightly glaucous, minutely but evenly striate, very pungent pointed; in coastal specimens commonly less than 10 cm. long. *Panicles* loose and, especially in stunted forms, subtended by the uppermost leaf sheath, which bears a reduced lamina. In stunted forms panicles about 5 cm. long but up to 25 cm. in taller specimens. Rhachis smooth or scabridulous, somewhat angular. *Spikelets* on pedicels 5-10 mm. long, compact and well filled, linear to linear-lanceolate in outline, 12-20 mm. long, 8-12-flowered, the lemmas compactly distichous-imbricate. *Glumes* lanceolate or elliptical, glabrous or the lower rarely minutely puberulous towards the base, acuminate or acute, about equal in length, 7.5-10 mm. long (i.e. about as long as the lowest lemma), 3-5-nerved, the median nerve more prominent and forming a keel or the glume rounded on the back. *Lemmas* lanceolate, indurate, rounded on the back, pubescent with short, silky hairs at the base and along the lower half of the median line and for a variable distance up the margins, scabrid above, with 3 groups of 3 nerves each but the lateral nerves of the groups only visible towards the centre of the lemma. The lateral groups of nerves visible on the rounded sides of the lemmas when in the spikelet, the central one reaching the margin but not central to the lateral portion of the obtuse or ragged apex; lowest lemma 8-9 mm. long. Callus pubescent, 0.5 mm. long. *Paleas* elliptical,


B
C
D
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(a)
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(b)

Fig. 15.—(*a*) *Triodia irritans* var. *compacta*, from *Rogers*, Sept. 1907. (*b*) *T. irritans* var. *laxispicata* var. nov., from *Vickery*, 14.x.1949. Lettering as in previous figures.

membranous except for the hardened nerves which are ciliolate, pubescent in the lower half between the nerves, 7-8 mm. long (Fig. 15(*a*) *A-H*).

It is to this and to the following variety that Brown's name has been most generally applied in Australian literature. In this variety, found along the coast in South Australia but extending into the mallee areas of north-western Victoria, the plants tend to be low and spreading and the spikelets are plump and neatly distichous.

Distribution.—SOUTH AUSTRALIA: St. Francis I., Nuyt's Archipelago, *Drs. Verco and Torr*, Feb. 1909 (NSW); Venus Harbour, *Dr. R. S. Rogers*, Sept. 1907 (NSW); Elliston Beach, Eyre's Peninsula, *J. H. Willis*, 26.viii.1947 (HOLOTYPE) (MEL, CANB); between Port Lincoln and Coffin's Bay, *J. H. Maiden*, Jan. 1907 (NSW); Currency Creek, near Goolwa, *J. B. Cleland*, 14.xii.1935 (BRI). VICTORIA: Nullawil to Kalpinning (about 30 miles SE. of Lake Tyrrell), *W. Watts*, Nov. 1917 (NSW).

19a. **Triodia irritans** var. **laxispicata** var. nov.

Holotype.—Tooleybuc, *J. Vickery*, 14.x.1949.

Affinis *T. irritanti* R. Br. sed spiculis laxioribus, lemmatibus divaricatis, 4-7-floriferis.

Culmi glabri vel puberuli et scabriduli. *Foliorum vaginae* striatae, glabrae, glaucae vel puberuli. Orificia ciliata. *Laminae* conduplicatae, rigidae, glaucae vel puberuli, pungentes. *Panicula* angusta, laxa rhachis angulata; anguli scabri. *Spiculae* laxae, lineares, oblongae vel lanceolatae, pedicellatae; pedicelli ad 5 mm. longi (superioribus exclusis), 4-6-floriferae. *Glumae* oblongae, scabridulae vel glabrescentes, induratae, 3-7-nervis, medio nervo prominente, subaequales. *Lemmata* cartilaginea, lanceolata, obtusa vel subtruncata vel emarginata, ad basim villosa; carina et margines infra mediam partem villosi, apices ciliolati. *Paleae* ellipticae, membranaceae, carinis ciliolatis, infra mediam partem villosis.

Forming large glaucous tussocks, which may die away from the centre leaving rings of living culms. *Culms* glabrous or glaucous owing to a minute pubescence, especially near the upper nodes when they are extruded from the sheaths. *Leaf sheaths* minutely striate and glaucous. Under a 20x lens the glaucosity appears to be due to a minute pubescence. The orifice is almost glabrous except for the short erect cilia of the ligule. The petiole-like bases of the laminae are very scabrid on the adaxial surface. *Laminae* more than 10 cm. long. *Panicle* narrow but the lower branches are probably spread at anthesis. The angular rhachis is scabrid as are the filiform lateral branches of which the lowest carries up to 7 spikelets on short pedicels up to 5 mm. long though that of the terminal spikelet appears to be longer as it is more or less continuous with the last segment of the rhachis. *Spikelets* loosely oblong though when young the lemmas are closely imbricate with the margins of one folded over and embracing the base of the next above so that the outline is narrow lanceolate or cylindrical. Later the lemmas become quite free from one another and divaricate. There are 4-7-florets per spikelet. *Glumes* stiff and indurate, scabridulous, rounded on the back or the mid nerve prominent or the mid nerve and the shorter lateral nerves all slightly prominent. *Lemmas* broadly lanceolate and obtuse, the apex ragged, subtruncate or emarginate but the mid nerve never extending as a mucro, villous with silky hairs at the base, along the lower half of the median line and along half to two-thirds of the margin, the remainder of the dorsal surface being smooth or scabridulous and the upper margin ciliolate. The general texture is stiff but not as indurate as in *T. irritans* var. *irritans* and the groups of nerves are more readily seen. Of these the lateral groups appear as 2 or 3 greenish streaks close to but distinct from the margins. In the larger forms the whole spikelet is laterally flattened so that the lemmas are conduplicate but as most of those examined were empty this character is likely to vary. *Palea* elliptical, narrowed towards the apex, membranous, the nerves not so thickened as in *T. irritans* var. *irritans* but pubescent between them in a similar manner, about as long as the corresponding lemma and often extruding slightly beyond it.

The variety can be recognized by the loose spikelets with divergent but indurate lemmas. In order to cover the variations 3 forms are described below. As there are considerable differences in spikelet size no dimensions have been given in the above description.

Forma A.—This group includes the specimen nominated as a type of the variety. The measurements are as follows: *Panicle* 15-30 cm. long. *Spikelets* 10-15 mm. long, 5-7 mm. wide when the lemmas are spread. *Glumes* 5.5-9 mm. long. *Lowest lemma* 6-7 mm. long. *Palea* about as long as its lemma. (Fig. 15(*b*) *B-H*).

Distribution.—QUEENSLAND: Goondiwindi, *Dr. J. Shirley*, Nov. 1919 (NSW); Wyberba, Darling Downs district, *L. S. Smith*, No. 779, 29.i.1940; between Wyberba and Wallangarra, *C. T. White*, No. 9359, 13.x.1933 (BRI). NEW SOUTH WALES: Wood's Reef, Barraba, *H. M. R. Rupp*, Oct. 1913; Murrurundi, *W. F. Blakely*, 10.x.1911; Barnard River, 40 miles N. of Scone, *H. L. White*, 10.vii.1918; Curriecabark district, W. of Barrington, *E. L. Hyem*, Apr. 1947; Barrington district, *Hyem*, Sept. 1946; Warrumbungle Ranges, *W. Forsyth*, Oct. 1899; Harvey Range, Peak Hill, *J. L. Boorman*, Nov. 1905 (NSW); W. of Balranald, *D. L. W. Henderson*, No. 445, 5.x.1947; Murray Downs, *D. L. Henderson*, No. 446, 18.x.1947; Balranald, *D. L. W. Henderson*, No. 333, 5.x.1947; Tooleybuc, *J. Vickery*, 14.x.1949 (HOLOTYPE) (NSW, CANB).

Forma B.—This form covers the large-spikeleted specimens from the Flinders Range and other places in South Australia. It includes specimens that approach var. *irritans* on the one hand and forma *A* on the other. *Panicle* 15-25 cm. long. *Spikelets* 12-20 mm. long, 7-10 mm. wide when lemmas are spread. *Glumes* 8-12 mm. long, sometimes subscarious in texture. *Lowest lemma* 8-10 mm. long. *Palea* shorter than or about equal in length to its lemma (Fig. 16 (*a*)). A characteristic specimen of this form is that collected by the writer in the Port Germein Pass and another is Blake No. 16856 collected on the same date and in the same locality.

Distribution.—SOUTH AUSTRALIA: 70 miles N. of Quorn, *H. G. Andrewartha*, 23.ix.1936 (ADW); Mount Remarkable, *F. von Mueller* about 1847; Flinders Range, *Max Koch*, No. 771, Oct. 1901 (NSW); Flinders Range, Port Germein Pass, *S. T. Blake*, No. 16856, 28.viii.1946 (BRI) same locality, *N. T. Burbidge*, 28.viii.1946 (TYPE of form) (CANB); North Caltowie Hundred, *A. M. Acock*, 22.x.1941; Beetaloo Valley near Gladstone, *G. H. Clarke*, 25.ix.1936 (ADW); Hallet, *J. B. Cleland*, 16.xi.1938 (BRI); Pallamana, NW. of Murray Bridge, *N. T. Burbidge*, 24.xii.1943 (ADW).

Forma C.—This is based on a few rather poor specimens mainly from southern Queensland. *Panicle* 10-25 cm. long. *Spikelets* 7-15 mm. long, 3-5 mm. wide. *Glumes* 5.5-7 mm. long. *Lowest lemma* 4.5-6 mm. long, shorter in relation to its breadth than in the above forms and often appearing more villose.

Distribution.—QUEENSLAND: Darling Downs district, Yelarbon, *S. L. Everist,* No. 914, 19.xii.1934; near Ballandean, *M. S. Clemens,* Sept. 1944 (BRI); New South Wales-Queensland border, *Phyllis Vickery,* 1933 (NSW).

20. **Triodia scariosa** sp. nov.; *T. irritans* N. T. Burbidge in J. Roy. Soc. W. Aust. **30**: 25 (1946) non R.Br.

Holotype.—Pioneer Rock, N. of Lake Cowan, *N. T. Burbidge,* No. 2675.

Affinis *T. irritanti* R. Br. sed spiculis laxioribus, minoribus, glumis et lemmatibus scariosis.

Culmi graciles rigidi. *Foliorum vaginae* glabrae, induratae, striatae. Orificia glabra sed ligulae cum brevibus cillis. *Laminae* cum brevibus petiolis, conduplicatae, glaucae, striatae, rigidissimae, pungentes. *Panicula* angusta, 12-30 cm. longa, rhachis scabridula. *Spiculae* lineares vel lanceolatae, laxae, 4-9-floriferae, 9-16 mm. longae, 3-6 mm. latae, pedicellatae; pedicelli scabriduli. *Glumae* scariosae, lanceolatae, acutae vel acuminatae, aequales, 5-8 mm. longae, 1.5-2.5 mm. latae, 3-5-nervis, medio nervo prominente. *Lemmata* scariosa vel membranacea, lanceolata, apices emarginati, ciliolati, ad basim villosa; margines villosi; nervi medii mucronulati; infima lemmata 5-8 mm. longa; callus villosus, 0.5 mm. longus. *Paleae* membranaceae, ellipticae, 4-7 mm. longae, bases villosae, carini ciliolati.

Forming hemispherical or flat-topped tussocks, which may become ring-like or crescentic when old. *Leaves* pale greyish green but not minutely puberulous under a 20x lens as in *T. irritans* var. *laxispicata.* Orifice with dense short cilia on the ligule but the outer edge glabrous or with similar hairs. *Panicle* narrow but loose, the rhachis with alternate slender branches that bear shortly pedicellate spikelets, some of which are along capillary tertiary branchlets. The rhachis is minutely scabrid or almost smooth. *Spikelets* loose though when young the lemmas embrace closely as in the above variety. *Glumes* thinly scarious and almost membranous, nerves prominent, especially the median one, apex usually acute or acuminate but in Calaby's material where the spikelets are smaller the apices are sometimes almost obtuse or ragged. *Lemmas* scarious or membranous, linear-lanceolate or lanceolate in outline; the apex emarginate with a minute slender mucro between the membranous lateral lobes, or the mucro absent and the apex ragged or truncate; nerves in each group closely proximate so that the lemmas appear to have 3 thick, prominent nerves of which the laterals form a ridge close to the margin in the upper half and reach the top on the outer side of the lateral lobes. The bases of the lemmas are villose with silky hairs that continue up about the lower third to half of the median line as well as for at least the lower two-thirds of the area between the margin and the lateral nerve group. The rest of the dorsal surface scabrid or glabrous but the upper margin ciliolate. Callus villose and, in the spikelet, hidden by the

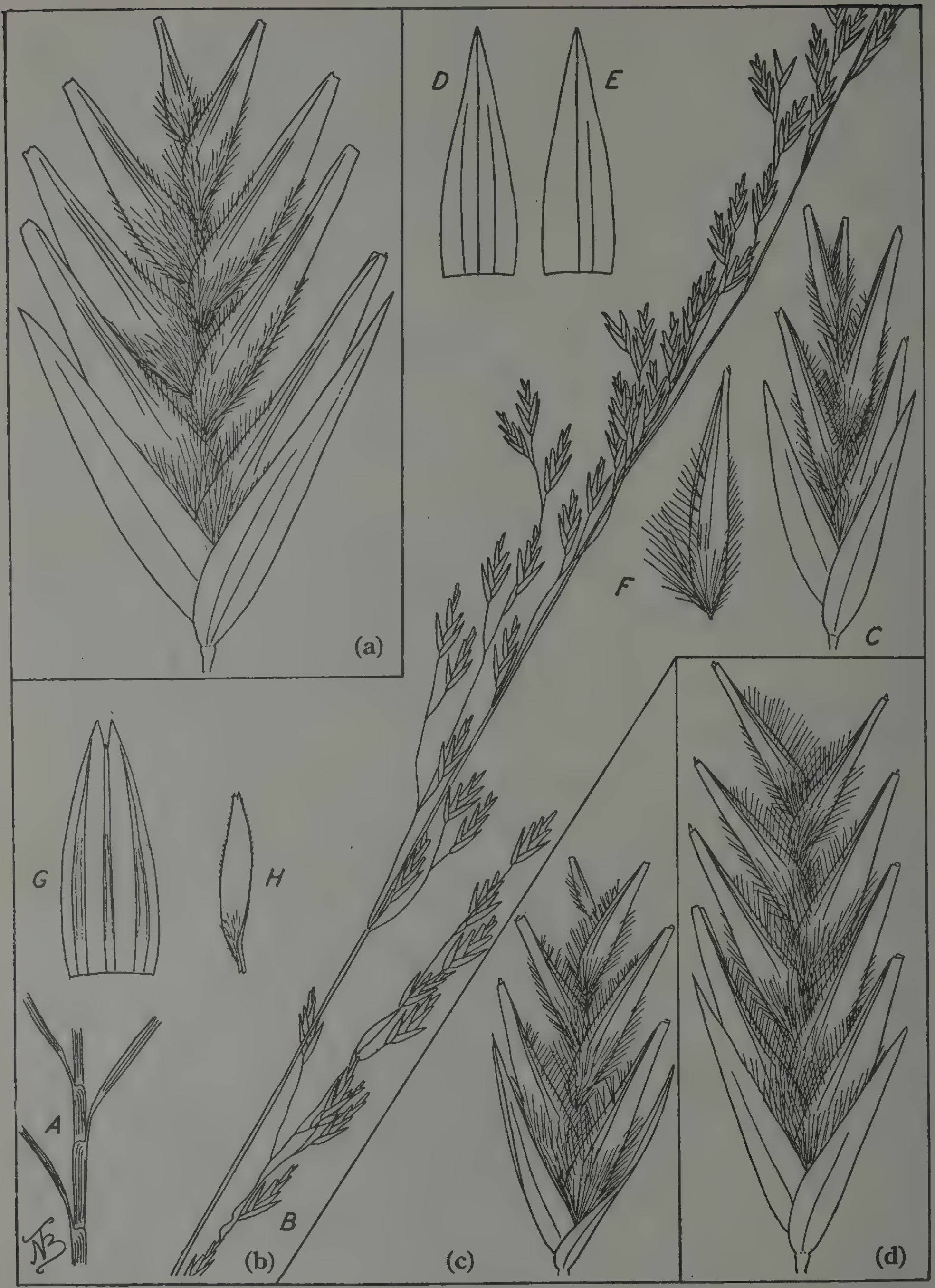

Fig. 16.—(*a*) *Triodia irritans* var. *laxispicata* forma B, from *Burbidge*, 29.viii.1943. (*b*) *T. scariosa* sp. nov., from *Burbidge*, No. 2675. (*c*) *T. scariosa* sp. nov., from *Henderson*, No. 444 (showing divaricate mature lemmas). (*d*) *T. scariosa* sp. nov., from *Gardner*, No. 808. Lettering as in previous figures.

tuft of hairs on the top of the rhachilla joint. *Paleas* slightly shorter than their lemmas, elliptical or linear, membranous in texture, nerves ciliolate and the base usually villose though not always so in Western Australian material. *Anthers* 3, purplish, 2.75-3 mm. long (Fig. 16(*b*)-(*d*)).

In the revision of the Western Australian material this was included under *T. irritans* R. Br. but further study of the eastern specimens shows that it is distinct. It extends from the semi-arid *Eucalyptus* forests of south-eastern Western Australia through South Australia to western New South Wales and north-eastern Victoria. The eastern and western specimens show much the same amount of variation but those collected by Calaby are smaller in most of their dimensions and the spikelets are bronze-purple whereas in other material they are greyish with some purple tinting. The area of distribution is interrupted by the northward extension of the Flinders Range but possibly future collections will fill in this gap.

Distribution.—WESTERN AUSTRALIA: near Meekatharra, *C. A. Gardner*, July 1927; sand-heath near Coorow, *C. A. Gardner*, Dec. 1930 (PERTH); Southern Cross, *J. H. Maiden*, Sept. 1909 (NSW); 20 miles E. of Mount Holland, *C. A. Gardner*, Aug. 1929; 1 mile E. of Boorabbin, *C. A. Gardner*, No. 7996, 20.x.1945 (PERTH); 5 miles W. of Kalgoorlie, *N. T. Burbidge*, No. 1918, 18.viii.1947 (CANB); Kalgoorlie, *C. A. Gardner*, No. 808, 21.ix.1920 (PERTH); Boulder City, *W. V. Fitzgerald*, Oct. 1898 (NSW); Pioneer Rock, N. of Lake Cowan, *N. T. Burbidge*, No. 2675 (HOLOTYPE) (CANB); Southern Hills, Fraser Range, *C. A. Gardner*, Nos. 2851, 2851*a*, 20.x.1931 (PERTH); 15 miles W. of Zanthus, *J. Calaby*, 26.x.1947 (CANB). SOUTH AUSTRALIA: Immarna railway siding, *J. Calaby*, No. 6, 19.x.1947; 15 miles E. of Immarna, *J. Calaby*, 18.x.1947; 16 miles E. of Immarna, *J. Calaby*, 18.x.1947 (CANB). NEW SOUTH WALES: Stephens Creek, Broken Hill district, *A. Morris*, 7.viii.1921; Menindie, *J. Granton*, Sept. 1910 (NSW); N. of Wentworth on the Pooncarrie road, *D. L. W. Henderson*, No. 444, 1.xii.1947 (NSW, CANB); Wentworth, *T. McCullock*, 20.xi.1920; Byrock, *J. L. Boorman*, Nov. 1903 (NSW); 6-7 miles NW. of Condobolin, *K. H. L. Key*, 6.x.1937 (CANB); Molong, *J. H. Maiden*, Sept. ; Lachlan district, *T. Duff*, 1882 (NSW); Goolgowi-Rankin Springs, about Ulonia Gap, *D. L. W. Henderson*, No. 235, 20.xii.1946 (NSW, CANB); Moomboodool, *E. N. McKie*, 20.xii.1920 (NSW). VICTORIA: between Euston and Mildura, *J. Vickery*, 18.viii.1946 (NSW); Boundary Bend, *D. L. W. Henderson*, No. 411, 5.x.1947 (NSW, CANB); Nandaly, *W. Watts*, No. 334(*a*), Sept. 1917 (NSW).

21. **Triodia lanata** J. M. Black in Trans. Roy. Soc. S. Aust. **40**: 57 (1916).

Holotype.—In scrub at Minnipa, J. M. Black, Nov. 1915.

Forms dense hemispherical "pincushion" tussocks about 45 cm. in diameter. *Culms* short, much branched. *Leaf sheaths* tomentose with woolly hairs, older sheaths glabrescent, 2-3 cm. long. Orifice and ligule with woolly hairs like those of the sheaths. *Laminae* very rigid and pungent pointed, glabrous except adjacent to the orifice, 5-12 cm. long, 1 mm. in diameter, conduplicate and appearing terete, minutely but evenly striate under a 10x lens. Panicle open, with a slender, minutely scabridulous rhachis. *Spikelets* not numerous, on slender pedicels up to 1 cm. long, ovate to lanceolate, 5-7-flowered, 8-13 mm. long. *Glumes* villous or with sparse hairs, broadly lanceolate acute or acuminate, scarious, purplish or brownish and becoming straw-coloured when old, 7-10 mm. long; lower 1-3-nerved, upper 3-nerved. *Lemmas* scarious or membranous, 6-8 mm. long, with an obtuse, ragged or minutely mucronate apex, densely silky pubescent with hairs up to 2 mm. long in the lower half, callus minute and densely pubescent, nerves in the usual groups but the laterals of each group fading out so that the apex is 3-nerved. *Paleas* oblong-elliptical, membranous, 5-6.5 mm. long, ciliolate on the nerves and hairy between them in the lower two-thirds, notched at the apex or the apex split between the nerves. *Anthers* 2 mm. long (Fig. 14(*b*)).

The illustration given of this species is taken from Mr. Black's original plate as the type specimen was not available at the time the figures were prepared. In Calaby's specimen the lower glume is glabrous or slightly scabrid while the upper is sparsely villous in the lower half.

Distribution.—SOUTH AUSTRALIA: 15 miles E. of Barton, *J. Calaby,* 17.x.1947 (CANB) (not typical); Minnipa, *J. M. Black,* 1915 (HOLOTYPE) (MEL).

22. **Triodia roscida** sp. nov.

Holotype.—One mile SE. of Turner Station, Kimberley district, *R. A. Perry,* No. 2404, 9.vii.1949.

Affinis *T. wiseana* C. A. Gardn. sed laminis guttas sudantes, lemmata pubescentiora, spiculae 3-4-floriferae.

Foliorum vaginae sparse villosae. Orificia barbata, villis 2-3 mm. longis. Ligulae breves, ciliatae. *Laminae* rigidae pungentes, striatae, roscidae; margines ciliolati. *Panicula* angusta, 15-25 cm. longa; rhachis et rami scabriduli. *Spiculae* 3-4-floriferae, breves pedicellatae, oblongae vel cuneatae, 6-9 mm. longae. *Glumae* rigidae, oblongae vel lanceolatae, acutae, aristulatae, glabrae vel scabridulae, subaequales, 4.5-7 mm. longae, cum 5-7-nervis. *Lemmata* pubescentia, oblonga, trilobata; lobi angusti, subulati, rigidi, glabri vel scabriduli, ciliolati, subaequales, 1.5-2 mm. longi; lemmata infima 6-8 mm. longa (lobis inclusis), callus minutus. *Paleae* membranaceae, glabrae sed ad basim pubescentes, carinis alatis, alis angustis, ciliolatis; infimae 5-6 mm. longae.

Forming large, dense tussocks (No. 2342—"3 feet in diameter, 18 inches high"; No. 2404—"10 feet in diameter, 3-4 feet high"), the flowering heads protruding 2-3 ft. above the rest of the plant. *Culms* branched in the usual manner, nodes glabrous but normally concealed by the sheaths. *Leaf sheaths* rounded on the back, sparsely villous with scattered hairs, minutely striate. Orifice with a tuft of erect but flaccid hairs of the same type as those on the sheath. Ligule a short, dense row of cilia. *Laminae* with distinct petiole-like bases, which are villous on the adaxial surface, the hairs being continued more sparsely along the margins almost or quite to the apices. The abaxial surface of the rigid, conduplicate, pungent-pointed laminae evenly but minutely striate and with scattered globules of a brownish secretion that give a bedewed appearance to the plant. This secretion is also present on the lobes of the lemmas in No. 2404 but not in No. 2342 where the material is older. It also appears more scantily on the younger leaf sheaths and at the tips of some paleas. *Panicles* narrow and with short, alternate branches bearing shortly pedicellate spikelets, which are loosely secund though not conspicuously so, the lowest branches bearing 4-7 spikelets. *Spikelets* somewhat cuneate in outline owing to the spreading of the upper parts but apparently oblong in the earlier stages. *Glumes* rigid, indurate, oblong to lanceolate, the apices acute and the mid nerve extending as a short ciliolate mucro, subequal, 4.5-7 mm. long and with 2 or 3 smaller nerves on either side of the prominent mid nerve; glabrous except when the lower glume is faintly scabridulous, straw-coloured or pale with purplish apices. *Lemmas* 3-4, lowest 6-8 mm. long, the basal part oblong or oblong-lanceolate and boat-shaped, densely pubescent with soft hairs on back of entire portion, slightly constricted below the 3 subulate, glabrous, and ciliolate lobes, which may be purplish. There is a minute callus at the base. *Paleas* glabrous, narrow and elliptical or elliptical-lanceolate, slightly shorter than the corresponding lemma, very narrowly winged on the nerves, wings ciliolate (Fig. 11(*a*) *A-H*).

In comparison with other species this can be readily recognized by the globules of secretion on the leaf blades, a character not observed in any other species up to the present, and by the pubescent lemmas with the boat-shaped base and slight constriction below the 3 short and subulate lobes. The secretion from the leaves does not seem to be very sticky and does not resemble the resin formed on the leaves of the species grouped around *T. pungens* and *T. mitchelli* sens. lat. The structure of the panicle suggests some affinity with *T. fitzgeraldii* and *T. racemigera.*

Distribution.—WESTERN AUSTRALIA: 1 mile SE. of Turner Station, Kimberley district, *R. A. Perry,* No. 2404, 9.vii.1949 (HOLOTYPE). NORTHERN TERRITORY: 16 miles S. of Limbunya Station (W. of Wave Hill), *R. A. Perry,* No. 2342 (CANB).

23. **Triodia triticoides** C. A. Gardner, Flora W. Aust. 1(1): 78 (1952).

Holotype.—Ord River, Kimberley, *E. C. B. Langfield,* No. 32, 28.i.1949.

Culms puberulous. *Leaf sheaths* puberulous, especially on exposed portions, minutely striate or almost smooth. Orifice ciliate with hairs similar to those of the densely ciliate ligule. *Laminae* with a narrow petiole-like base, glabrous, pale green, slender, and up to 40 cm. long. *Panicle* narrow, 20-40 cm. long, rhachis scabridulous, slightly hollowed behind each of the alternate lateral branches, of which the lowest is 4-7 cm. long and with 12-17 spikelets. *Spikelets* distichously secund on the branches, ovate or lanceolate, laterally compressed but well filled, 7-10-flowered. *Glumes* oblong, boat-shaped, 4-4.5 mm. long, indurate with a prominent mid nerve and one or two obscure laterals on either side, equal in length but the lower glume commonly asymmetrical at the apex, the abaxial side having a short lobe about as long as or longer than the short mucro. *Lemmas* ovate-lanceolate in outline, indurate, with short, soft hairs along the median line in the lower half and near the margins towards the base, which has a few scanty hairs; apices trilobate, the mid lobe slightly shorter and narrower than the laterals, the nerves forming a thickened area in each lobe but obscure below; lowest lemma 4-5 mm. long. *Paleas* elliptical, membranous, glabrous, about as long as their lemmas, the nerves with well-developed wings. *Lodicules* obovate or cuneate (Fig. 17(*a*) *A-H*).

Distribution.—WESTERN AUSTRALIA: Kimberley Research Station, Ord River, *E. C. B. Langfield,* No. 32, 28.i.1949 (HOLOTYPE) (PERTH, CANB); Lookout Hill, Kimberley Research Station, *R. A. Perry,* No. 2661, 30.vii.1949 (TOPOTYPE); Point Spring, 30 miles E. of Carlton Station, *R. A. Perry,* No. 2654, 29.vii.1949 (CANB).

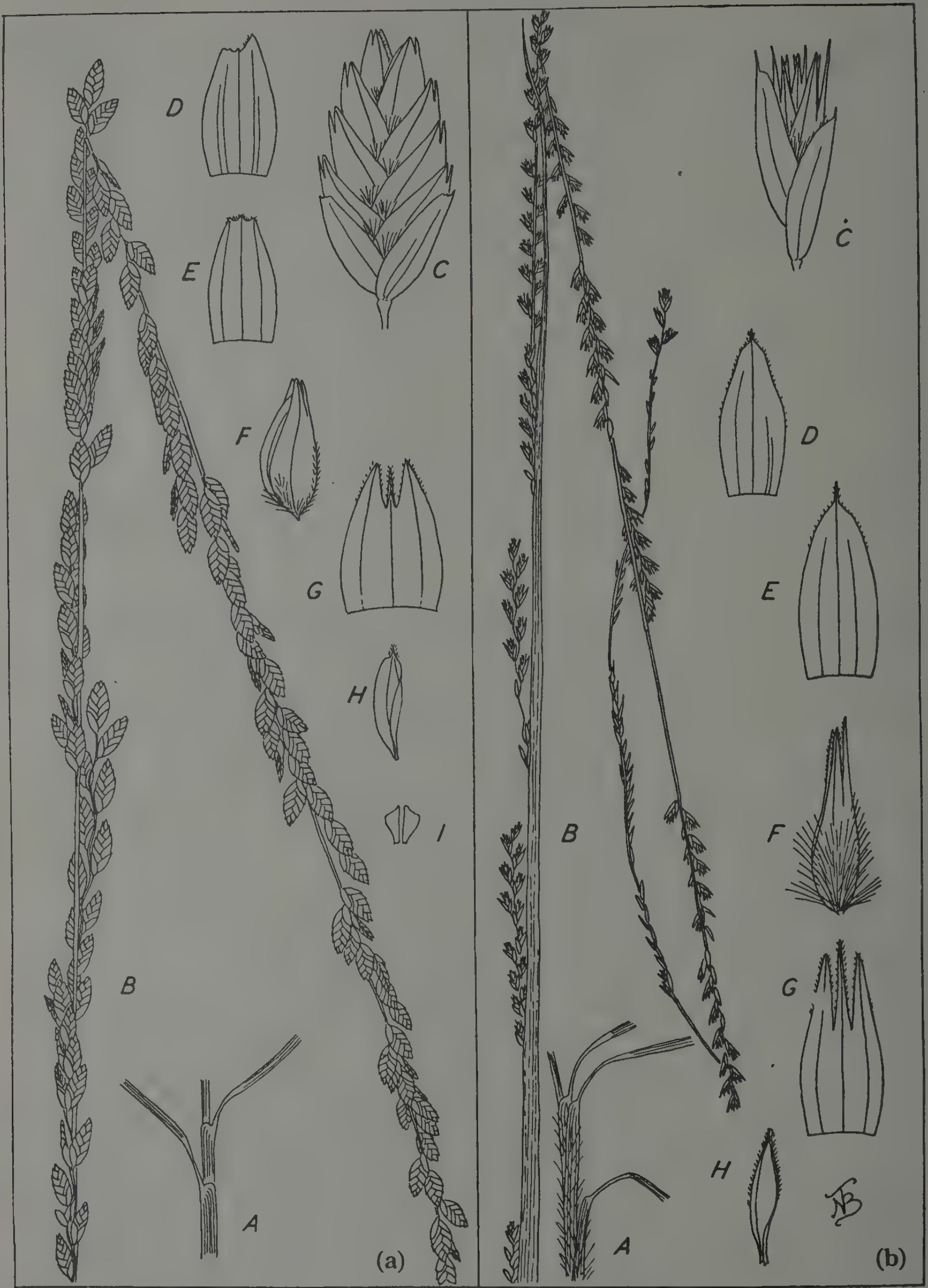

Fig. 17.—(*a*) *T. triticoides* C. A. Gardner, from *Langfield*, No. 32. (*b*) *T. racemigera* C. A. Gardner, from *Durack* 1945. (Co-type specimen; note that portion of the panicle is malformed and the spikelets not fully developed.) Lettering as in previous figures.

24. **Triodia racemigera** C. A. Gardner, Flora W. Aust. 1(1): 77 (1952).

Holotype.—Ord River, Kimberley, *K. M. Durack,* Apr.-May 1945.

Culms rigid, glabrous. *Leaf sheaths* light brown, villous-pubescent with silky hairs on the abaxial surface, upper ones glabrescent above. Orifice with short, very dense cilia. *Laminae* not as rigid or as thick as in *T. fitzgeraldii* but otherwise similar. *Panicle* 40-50 cm. long, very narrow owing to the erect, alternate lateral branches, which are 2-3 cm. long and adpressed to the main rhachis in the dry specimen. *Spikelets* subsessile or very shortly pedicellate, distichously secund along the branches, laterally compressed, 4.5-6 mm. long, 2-3 mm. wide, pale, 3-flowered. *Glumes* indurate, oblong-lanceolate or lanceolate, mucronate, keeled slightly by the mid nerve, glabrous; lower 1-3-nerved, sometimes with an additional lateral, 4.5-5 mm. long, upper 3-nerved, the laterals fainter below, 5-5.5 mm. long. *Lowest lemma* broadly lanceolate, indurate, deeply 3-lobed, 5-5.5 mm. long, villous in the lower half, glabrous above and on the narrow, stiff lobes, margins ciliate above, callus minute. *Paleas* narrow-lanceolate or elliptical, the apex fitting into the concavity of the mid lobe of the lemma, 3.5-4 mm. long, the nerves narrowly winged and minutely ciliolate (Fig. 17(*b*) *A-H*).

The species, of which only the co-type specimen has been seen, shows a close affinity with *T. fitzgeraldii,* particularly in the vegetative characters though the culms and leaves are more slender. The panicle is of the type seen in that species and also in *T. triticoides, T. secunda,* and *T. angusta* though the small but indurated spikelets with deeply lobed lemmas make it easy to distinguish.

Distribution.—Ord River, Kimberley district, *K. M. Durack,* Apr.-May 1945 (HOLOTYPE) (PERTH).

25. **Triodia fitzgeraldii** N. T. Burbidge in J. Roy. Soc. W. Aust. 30: 25 (1946).

Holotype.—Dillon Springs, East Kimberley, *W. V. Fitzgerald,* No. 1643, Oct. 1903.

Culms very rigid, glabrous. *Leaf sheaths* brown, minutely pubescent with adpressed hairs on the abaxial surface, the margins hirsute with shining hairs up to 2 mm. long. The older sheaths glabrescent. Orifice with hairs similar to those of the margin. Ligule a dense row of cilia shorter than those on the ridges of the orifice. *Laminae* rigid, minutely but evenly striate, very stiffly pungent pointed, glabrous and with a dull appearance, conduplicate and appearing terete. *Panicle* narrow with numerous shortly pedicellate or subsessile spikelets loosely secund along distant alternate branches which are up to 6 cm. long, rhachis minutely scabridulous. *Spikelets* laterally compressed, linear, 4-6 mm. long, 3 mm. wide, pale but probably purplish when young, 4-6-flowered. *Glumes* scarious or membranous, oblong-lanceolate, obtuse or acute, subequal, margin minutely ciliolate, 1-nerved or rarely with a pair of short laterals, 2.5-3.5 mm. long. *Lemmas* lanceolate, thinly scarious, 3-nerved, 3-lobed, the median lobe narrow-acuminate, the laterals acute and thinner, margins ciliolate. Callus minute and with a ring of hairs at the junction with the lemma, which is otherwise glabrous except for a few hairs on the lower part of the median line. *Palea* 2 mm. long, narrowly winged on the nerves (Fig. 18(*a*) *A-H*).

This species is known only from the type locality and from the type material. It was described from a sheet in the State Herbarium in Perth but another sheet of the same collection is in the Sydney Herbarium. The species shows a definite affinity with the last 2 species but is quite distinct owing to the scarious and loosely arranged spikelets.

Distribution.—Dillon Springs, East Kimberley, W.A., *W. V. Fitzgerald,* No. 1643, Oct. 1906 (HOLOTYPE) (PERTH, NSW).

26. **Triodia angusta** N. T. Burbidge in J. Roy. Soc. W. Aust. **30:** 27 (1946).

Holotype.—Coongan Station, *Anderson* (Burbidge No. 452).

Tussocks hemispherical but rather loose and with radiating stolons, each of which has a terminal tuft of shoots (cf. Burbidge 1945*b*, Plate xxii, Fig. 1). *Culms* rigid, glabrous. *Leaf sheaths* smooth or minutely striate, glaucous. Orifice with a very short series of erect hairs similar to those of the ligule. *Laminae* rigid, glaucous, conduplicate and appearing terete, margin scabrid, at least in the lower part. *Panicle* narrow with sessile spikelets spicate and secund along slender, alternate branches lateral to the main rhachis. *Glumes* lanceolate, scarious or membranous, lower 1-nerved, upper 1-3-nerved, 3-4 mm. long, both acuminate or aristulate. *Lemmas* scarious or membranous, lanceolate or narrowly ovate, shortly 3-lobed, 3-nerved, glabrous except for a few hairs at the base and rarely a few on the margins; lowest 2.5-3 mm. long. *Paleas* oblong or elliptical, membranous or scarious, nerves ciliolate (Fig. 18(*b*) *A-H*).

The species is closely related to *T. secunda* and shows some affinity with the species last described. It is also noticeable that in this group it is the upper glumes which have the larger number of nerves rather than the lower as it is in *T. procera, T. microstachya, T. cunninghamii,* and *T. stenostachya*, which also have small spikelets. It is considered likely that these two series have had different origins even though they all occur in the extreme north and northwest of the continent.

Distribution.—Western Australia between the Fortescue and De Grey Rivers. Localities are given with the type description.

27. **Triodia secunda** N. T. Burbidge in J. Roy. Soc. W. Aust. **30:** 26 (1946).

Holotype.—Coongan Station, *Anderson* (Burbidge No. 640).

The tussocks usually consist of spreading culms with long, tangled stolons ending in tufts giving rise to further series of stolons. *Culms* rigid and glabrous. *Leaf sheaths* pale or straw-coloured, glabrous. Orifice with an erect, fringed appendage into which several of the nerves of the sheath extend. Ligule a row of short cilia as in other species. *Laminae* narrower than the sheath, glabrous, dark green when fresh, minutely but evenly striate, conduplicate and appearing terete, stiffly pungent pointed, 6-12 cm. long. *Panicle* narrow with spikelets sessile and secund along distant alternate branches. *Spikelets* 3-6-

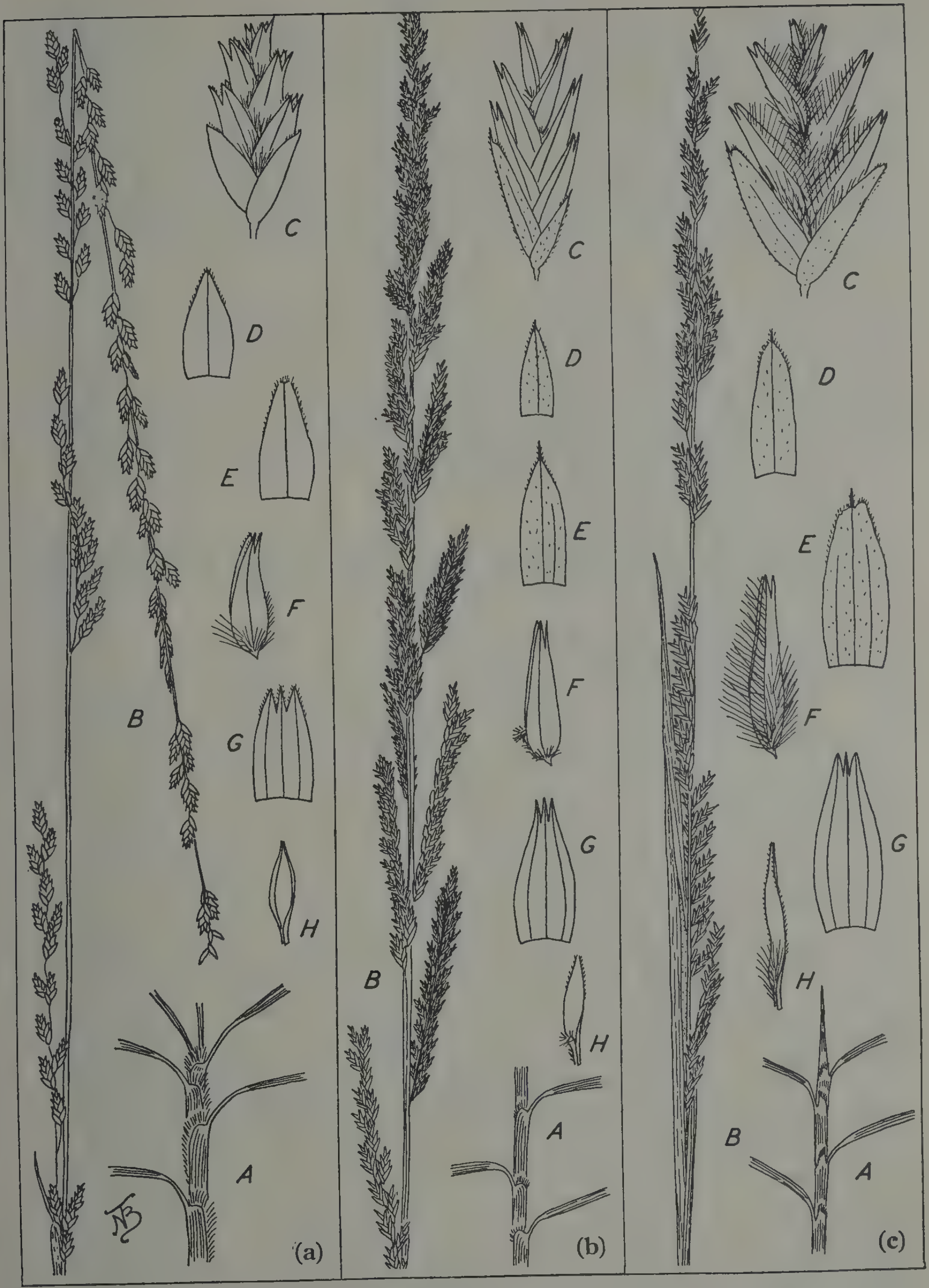
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Fig. 18. (*a*) *Triodia fitzgeraldii* N. T. Burbidge, from co-type material at Sydney. (*b*) *T. angusta* N. T. Burbidge, from *F. Melville*, 17.iii.1941. (*c*) *T. secunda* N. T. Burbidge, from *G. F. Melville*, Warralong Station. Lettering as in previous figures.

flowered. *Glumes* linear or lanceolate, scarious, 1-nerved or the upper with a pair of faint laterals, aristulate or the upper with a thin enervate lobe on either side, nerves scabrid; lower 3-4 mm. long, upper 4-5 mm. long. *Lemmas* lanceolate, membranous or scarious, 3-nerved, trilobate; the lobes acute and the median one little more than an extension of the mid nerve; with hairs at the base on the junction with the minute callus and also up the median line and along the submarginal portion near the lateral nerve; lowest lemma 3-5 mm. long. *Palea* linear, elliptical or slightly oblanceolate, pubescent at the base and scabrid on the nerves; lowest 3-5.3 mm. long (Fig. 18(*c*) *A-H*).

Distribution.—De Grey River area in north-west Western Australia; for localities see type description. The following specimen has also been seen: Port Hedland, *W. V. Fitzgerald,* July 1906 (NSW).

The peculiar fringed appendage at the orifice and the hairy secund spikelets make it very distinct. Owing to the former character it can be recognized in the field even when panicles are absent.

28. **Triodia spicata** sp. nov.

Holotype.—Napperby, about 100 miles NW. of Alice Springs, Northern Territory, *S. L. Everist,* No. 4188, 24.i.1950 (BRI, CANB).

Foliorum vaginae marginibus villosae. Orificia barbata, villis 2-4 mm. longis, flaccidis. Ligulae breves, ciliatae, *Panicula* angusta, spicata, 6-9 cm. longa. *Spiculae* biseriatae, divaricatae, 5-7-floriferae, sessiles, lanceolatae vel ellipticae, 9-13 mm. longae. *Glumae* induratae, subaequales, acutae vel obtusae, 4-5 mm. longae, cum 5-7-nervis. *Lemmata* lanceolata, acuminata, indurata; lemmata infima 5-6 mm. longa. *Paleae* membranaceae, glabrae, carinis alatis, alis angustis integris; infimae 5-6 mm. longae.

According to the collector's notes the plants are common on quartzite hills in the locality given and form compact tussocks up to 1 m. in diameter and half that in height. *Culms* branched in the usual manner, the nodes concealed by the sheaths on which the recurved bases of the older laminae are persistent. *Leaf sheaths* rounded on the back and with marginal fringes of rather flaccid, not woolly, hairs which form loose tufts up to 4 mm. long at the orifices. The ligule is ciliate and rather longer than in most species. *Laminae* conduplicate, slender, pungent pointed, 7-12 cm. long, less than 1 mm. in diameter, glabrous except for a few hairs (like those of the orifice) on the slender petiole-like base. *Panicle* a narrow spike with biseriate, sessile spikelets. *Spikelets* lanceolate or elliptical, sometimes slightly falcate. *Glumes* indurate, broadly lanceolate or ovate, 5-7-nerved but the lateral nerves often obscure, especially on the adaxial side of the lower one. The apices acute or obtuse but mostly torn or split in the type. *Lemmas* similar in texture to the glumes, remarkable in the genus for being acuminate, not lobed, glabrous except for a few short hairs on the lower part of the mid nerve, 3-nerved but each nerve with faint subsidiaries; the mid nerve prominent and forming a slight keel, the laterals near the margins; the apices usually split. *Paleas* linear or elliptical, glabrous, apices obtuse; nerves narrowly winged; wings entire, visible in the spikelets.

The type of panicle and the lack of lobing in the lemma make it so distinct that either the generic concept had to be widened or a new genus described. As, however, the growth habit, leaf type, and nervation of the lemma are entirely typical for *Triodia* and the other features are merely the logical result of tendencies already observed in other species, the former course has been adopted. The hairs of the orifice are similar to those of *T. wiseana* var. *brevifolia* but, apart from this, the spikelet characters are so distinctive that it is not possible to indicate the closest affinity with any degree of certainty. The species is known only from its type material.

ACKNOWLEDGMENTS

The writer wishes to express her thanks to the officers of the following herbaria for the loan of a great deal of material and for the assistance so freely given on a number of occasions: Botanic Museum and Herbarium, Brisbane; New South Wales National Herbarium, Sydney; National Herbarium of Victoria, Melbourne; Botany Department and Waite Agricultural Research Institute, University of Adelaide. Also to Mr. C. A. Gardner, State Herbarium of Western Australia, Perth, for the loan of material of his new species *T. racemigera* and for information on a number of points regarding Western Australian material.

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BOTANICAL CONTRIBUTIONS OF THE NORTHERN AUSTRALIA REGIONAL SURVEY

I. STUDIES ON NORTHERN AUSTRALIAN SPECIES OF EUCALYPTUS

By S. T. BLAKE*

(*Manuscript received October* 12, 1950)

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Summary

This is the first botanical contribution from the C.S.I.R.O. Northern Australia Regional Survey. Revised accounts of 50 species with discussions on taxonomy, distribution, and typification of names are the result of a partial revision of the genus *Eucalyptus* as represented in the northern part of Australia; keys to two groups particularly studied are given. All the 42 species known from the northern part of the Northern Territory are treated, with three keys to their identification; the first of these is based on characters observable in the field, the second on hand specimens with buds and flowers, and the third on hand specimens with fruits only. New criteria for the discrimination of species have been used, and some examples of their application are shown graphically; these include the number of lateral veins in the leaf, the ratio of its length to its breadth, and (to some extent) the exact distance of the intramarginal vein from the margin and the shape of the free part of the calyx-tube of the flower. The juvenile stages, flowers, fruits,

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* Queensland Herbarium, Brisbane, seconded as Botanist to the C.S.I.R.O. Northern Australia Regional Survey (now Land Research and Regional Survey Section, C.S.I.R.O.), 1946-7, by the Queensland Department of Agriculture and Stock.

and seeds are described for the first time for some species. Types of all names, with the herbaria in which they are to be found, are cited, with reference to published figures, some of which appear for the first time in this paper. Several lectotypes are designated, and the guiding principles adopted for their selection are described. Citations of specimens are restricted to those collected in 1946-9 on the Northern Australia Regional Survey, to types, new records, and some critical collections. Distribution maps of 51 species are based on all specimens examined. Plates from photographs illustrate the characteristic habit of some species, the deciduous nature of some, a few characteristic barks, various type specimens and some other specimens cited in taxonomic discussions.

The status of about 160 names was investigated. Among others, *E. clavigera* A. Cunn. ex Schau., *E. polycarpa* F. Muell., *E. terminalis* F. Muell., *E. foelscheana* F. Muell., and *E. racemosa* Cav. are shown to have been originally applied to species different from those currently passing under these names. Many names are treated as synonyms on taxonomic grounds, 24 of them for the first time. All nomenclatural changes are summarized in two tables. One new species, *E. porrecta* S. T. Blake, and one new combination, *E. gilbertensis* (Maiden & Blakely) S. T. Blake, are proposed. The following species are new records for the areas mentioned: *E. herbertiana* and *E. cliftoniana* (Northern Territory); *E. aspera* and *E. ferruginea* (Queensland); *E. bigalerita* and *E. patellaris* (Western Australia); and *E. dichromophloia* (South Australia).

In an appendix, the graphical methods and distribution maps are discussed and some remarks made on the phylogeny and history of distribution of the genus.

I. INTRODUCTION

The main purpose of this paper, the first botanical contribution of the Northern Australia Regional Survey, is an explanation of the names of species of *Eucalyptus* used in the account of the vegetation in "Northern Australia Regional Survey General Report on Survey of Katherine-Darwin Region, 1946" (C.S.I.R.O. Aust. Land Res. Ser. No. 1) and an account of the specimens of this genus collected during the expeditions of 1946, 1947, and 1948.

The eucalypts play a leading part in the taller vegetation of the region, and have been studied more intensively than any other group of plants in the area. However, during the examination of the collections, discrepancies were found to exist between the original descriptions and recent interpretations of some species. The only solution to this difficulty seemed to lie in a re-examination of the type specimens of as many species as possible. To a great degree this has been accomplished through the cooperation of several individuals and institutions. I examined a large series of specimens in the herbaria at Melbourne and Sydney in 1947 and 1949, and am indebted to the Directors of these institutions, Mr. A. W. Jessep and Mr. R. H. Anderson, for the loan of many types and other material. Mr. P. Bibby also assisted me in the search for some types during my visits to Melbourne. To Dr. M. R. Jacobs, Principal of the Australian

Forestry School, Canberra, I am indebted for the donation to the Queensland Herbarium of a nearly complete set of the specimens collected by him in the Northern Territory in 1933, and for the loan of many duplicates; this includes much type material. A number of specimens from Queensland and the Northern Territory has been sent for study by Miss N. T. Burbidge, Australian Herbarium, C.S.I.R.O., Canberra. Through the courtesy of the Director, Sir Edward Salisbury, and of Mr. V. S. Summerhayes, I have received photographs and fragments of specimens from the Herbarium of the Royal Botanic Gardens, Kew. Dr. J. B. Cleland lent his rich private collection. Also, I have had the opportunity to study and discuss the collections made by Mr. R. L. Specht on the Commonwealth of Australia — National Geographic Expedition to Arnhem Land, 1948, while they were being sorted. Many of the taxonomic problems encountered have been discussed with the other members of the staff of the Queensland Herbarium, namely the late Mr. C. T. White, Mr. W. D. Francis, Mr. S. L. Everist (who also tested the keys), and Mr. L. S. Smith, but the responsibility for the conclusions expressed in the paper is entirely mine. Photographs of herbarium specimens reproduced in this paper are the work of Mr. W. D. Sanderson, Department of Agriculture and Stock, Brisbane. The field photographs were taken by Mr. C. S. Christian, the leader of the expeditions, Mr. R. A. Perry, and myself. Mr. J. H. Simmonds (Officer-in-Charge, Science Branch, Department of Agriculture and Stock, Brisbane) suggested the statistical work carried out by Mr. P. B. McGovern and helped in other ways. My wife helped to check all the references and citations of specimens. After the typescript was completed, Miss M. B. Tindale (Australian Liaison Officer at Kew) sent photographs of, and notes on a number of specimens at Kew, Mr. C. A. Gardner lent specimens from the State Herbarium of Western Australia, Dr. H. J. Lam and Dr. C. G. G. J. van Steenis favoured me with the loan of the Malaysian material in the Rijksherbarium, Leiden, and Dr. R. Melville sent notes on some specimens at Kew and the British Museum of Natural History.

The results of the investigation have been very disconcerting, but they seem to be the only possible conclusions from the evidence available. Many adjustments in nomenclature are necessary, while the study of a wider range of material than has been available to previous students of the genus, rechecked at intervals during the past three years or so and qualified by observations in the field extending over a wide area of northern and north-eastern Australia, has led to revised concepts of several species, so that some names have been reduced to synonymy as the result of "lumping" and in a few cases specific status has been accorded groups previously otherwise treated. About 160 names and 70 accepted species are involved. The conclusions expressed are not likely to meet with universal acceptance; they are not necessarily final, and when the work of the Northern Australia Regional Survey is completed, sufficient material should be available for a reasonably thorough account of the eucalypts of Northern Australia.

The species of primary importance are those found in that part of the Northern Territory north of 20° S. lat., a region at one time called North Australia. Some species were originally found in the Kimberley Division of Western Australia or in Queensland, and it was essential to study specimens of these and other species from these areas for the clarification of the problems encountered.

New criteria for the discrimination of species have been studied and incorporated in revised descriptions of 50 species discussed in detail; special attention was paid to the number of lateral veins in the leaf and the ratio of its length to breadth. The number of pairs of lateral veins has proved a useful criterion in comparing and contrasting species in some groups, while the ratio of length to breadth provides a very satisfactory way of expressing differences in shape independently of size.

Peculiar problems were encountered, and the solution of some of them demanded an unusual approach. To assist their discussion, an outline of the history of advancing knowledge of the genus in the area has been presented, a number of terms defined, and an account given of the guiding principles adopted for the selection of lectotypes.

History

The name *Eucalyptus* was first published in 1789 when Charles Louis L'Héritier de Brutelle described the genus on p. 18 of his *Sertum anglicum seu plantae . . . imprimis in horto regio kewensi excoluntur* . . . and in t. 20 figured *E. obliqua* L'Hérit., the only species.* This species was described from specimens collected by David Nelson and William Anderson at Adventure Bay on Bruny Island, off the south-east coast of Tasmania, in January 1777, during Cook's third voyage. In the previous year, Joseph Gaertner had described and figured fruits and seeds of four species in the first volume of his *De fructibus et seminibus*, pp. 170-1 and 174, and tt. 34-5, under the genera *Metrosideros* and *Leptospermum*. The fruits and their seeds were the only parts of the plants seen by Gaertner. They were given to Gaertner by Joseph Banks and were removed from specimens collected by Banks and Solander in 1770, during Cook's first voyage. Undoubtedly the first specimen of *Eucalyptus* to be collected is the one of *E. gummifera* (Gaertn.) Hochr. collected by Banks and Solander at Botany Bay in April-May 1770, and now at the British Museum of Natural History, London; from a fruit of this Gaertner described and figured *Metrosideros gummifera*, deriving his specific epithet from a MS. note of Solander's.

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* The usually quoted date of publication is 1788. According to Buser, ex Mez in DC. *Monogr. Phan.* 9: 952 (1896) and ex O. Kuntze *Rev. Gen. Pl.* 3 (2): 157 (1898), the work did not appear until 1789.

Since 1788, over 1000 names have been applied to plants that have been referred to this genus, some of which have been based on the study of young plants raised in European gardens, and a few have been based on fossils that were supposed to represent species of the genus. This represents a great amount of exploration, observation, and description over the past 160 years.

Some knowledge of the history of the discovery and the classification of the eucalypts was found necessary for both the appreciation and the solution of some of the problems discussed in the following pages. The subject is a lengthy one and is only partly covered by Maiden in various parts of his "A Critical Revision of the Genus *Eucalyptus*" up to 1928. A brief account of the work of the chief investigators of the genus is given here, insofar as this work is closely associated with species of the northern part of the Northern Territory. For the most part this account was prepared independently of Maiden's work (for reasons which may be evident later on in this paper), and it contains matter that has not previously appeared in print. The chief stages are as follows:

1. The first collections were made by Robert Brown and Ferdinand Bauer along the shores of, and on the islands in the Gulf of Carpentaria in December 1802-March 1803, and by Allan Cunningham along the northern and western shores and the neighbouring coast of Western Australia in 1818-1821. None of these men published names in the genus, but Schauer studied their specimens and published some of Cunningham's manuscript names in 1843 in the second volume of Walpers' "Repertorium botanices systematicae." The collections of Brown and Bauer were made simultaneously. Bauer kept a personal set which later went to Vienna, and the names of some species were founded exclusively on specimens in this collection. There seems little chance of error in regarding the Brown specimens in the Brown herbarium (British Museum of Natural History), Kew, and different Australian herbaria as equivalent to duplicate types of these names. Maiden's figures of some of the Vienna specimens are exceedingly like the Brown specimens seen by me.

2. During the North Australian Expedition of 1855-56 led by A. C. Gregory, F. Mueller made detailed field observations of a number of species of which specimens were collected. The results were published in a paper in *J. Linn. Soc.* (*Bot.*) 3: 81-101 (1859), with the title "Monograph of the *Eucalypti* of Tropical Australia; with an Arrangement for the use of Colonists according to the Structure of the Bark." This was the first attempt at an arrangement based on the bark, but the specimens collected, or at least those that survived the hazards of travel, are often meagre in the extreme, and by themselves are a very poor basis indeed for the interpretation of the species described. However, the species were fully described in the field and these descriptions, together with the specimens, do provide a reliable basis of interpretation. Most of these collections are represented in the Melbourne Herbarium (National Herbarium of Vic-

toria), which owes its foundation to Mueller's personal herbarium. Of the collections made during the Gregory Expedition, duplicates of all were sent to W. J. Hooker at Kew; sometimes Mueller retained only fragments and sometimes everything was sent to Kew (cf. Hook. *Kew J.* **9**: 195, (1857), and Benth., Fl. Aust. **1**: preface, pp. 12* and 13* (1863)).

The localities cited by Mueller in his paper are often very generalized and it is frequently impossible to determine them without reference to the specimens themselves. The date of collection appears on most of the field labels, and it has been possible to localize the specimens by reference to Gregory's journal and map of the expedition in *J. R. Geogr. Soc.* 28: 1-137 (1858). The vague localities given by Mueller are sometimes even misleading; for instance, most of his references to the Roper River were found to belong to tributaries of the Katherine River.

3. In the third volume of his "Flora Australiensis," published in 1867,* Bentham gave an account of all species from Australia then known. An attempt was made to account for all species described up to that time. A considerable reduction in the number of recognized species resulted from treating a number of names as synonyms. Bentham's outstanding achievement in this genus was the sorting of a huge amount of material into some sort of order and the establishment of a major classification within the genus as a whole, the latter based on the structure and dehiscence of the anthers. Whatever may be the merits of Bentham's species-concept in the genus and whatever may be the faults of the so-called antheral system of classification, there is surely no one who cannot admire the tremendous achievement of bringing order out of chaos in this large and difficult genus.

4. Between 1879 and 1884 appeared F. Mueller's "Eucalyptographia" consisting of 10 decades of 10 plates, each representing species of the genus. A number of species occurring in the Northern Territory was figured or described or otherwise received mention. The separate plates are not numbered and the specimens from which the figures were drawn are not indicated. About the same time and later specimens were collected for Mueller by M. and N. Holtze and P. Foelsche, chiefly in the neighbourhood of Darwin.

5. Between 1903 and 1933 appeared the monumental "A Critical Revision of the Genus *Eucalyptus*" of J. H. Maiden, published at intervals in 74 parts arranged in eight volumes. In this extensive work are to be found excellent figures and long discussions of all known species, with copies or translations of the original descriptions. Synonyms and reputed synonyms are discussed under each accepted name and many features of the genus are described, but a complete synthesis of knowledge was never attempted. One of the outstanding features of the work is the series of excellent plates (chiefly the work of Miss M. Flockton) on which

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* The date on the title page is 1866, but in *J. Soc. Bibliogr. Nat. Hist.* 1: 71 (1937), H. S. Marshall has shown from notes in Bentham's diary that the volume was not published until January 5, 1867.

are figured twigs or other salient parts of a huge number of specimens, including very many types; the source of each figure is cited. Seeds of many species are illustrated and a number of coloured plates portray seedlings of many species grown in Sydney from seed. A work of such scope written over such a long period of time is bound to contain some inconsistencies of treatment. Naturally, as the work progressed and further evidence accumulated, earlier ideas were modified and these modifications of opinion are duly recorded. But many who have used the work must have been bewildered by the far too many obscure passages, inconsistencies of statement or even contradictions on the same or neighbouring pages, faulty translations, mis-statements of fact, irrelevancies, and even personalities scattered through the 3013 pages of text.

6. The collections of G. F. Hill, H. I. Jensen, C. E. F. Allen, and W. Baldwin Spencer between 1911 and 1917 provided the background for Maiden's review of the genus in the Northern Territory as Appendix III to Ewart and Davies' "Flora of the Northern Territory" (1917) and also provided much of the material for the treatment of the species concerned in the "Critical Revision".

7. "A Key to the Eucalypts," by W. F. Blakely, appeared in 1934. This is the only attempt since Bentham's time to bring together in one volume descriptions of all accepted species and varieties, and as such is a very valuable and handy basis for further work. Three very useful additional features in the "Key" are firstly, reference is made under each species to figures in Maiden's "Critical Revision"; secondly, there is an explanation to each plate in the "Critical Revision" in terms of Blakely's species-concept; and thirdly, a list of published names is given in alphabetical order, with Blakely's interpretations thereof. Many complaints, both published and unpublished, have been made concerning this work, but nobody yet has produced anything to take its place. The "Key", as such, is not well arranged in some places and contrasting characters are not always used — sometimes because of imperfect knowledge of the species (Blakely himself was the first to admit that the "Key" was far from complete, that there were many imperfections, and that much work remained to be done in the genus. I had the privilege of corresponding with him during the early days of my interest in the genus, from about 1935 until his death in 1941, and had personal discussions on a few occasions). I believe, as do many others, that the antheral system of classification has been over-stressed to such an extent that it has become a master rather than a servant, and that some of the minor groups distinguished by Blakely rest upon, at the best, very intangible distinctions. Many species have been described from single individuals, which may have been hybrids or in some way abnormal, but the responsibility for this may rest partly with the collector in that he did not provide adequate field notes.

8. In 1933, M. R. Jacobs made a special study of the eucalypts in the Northern Territory. Most of the systematic results were incorporated

by Blakely in his "A Key to the Eucalypts", with new species and varieties described under their joint names. Jacobs also prepared a more detailed account under the title "A Survey of the Genus *Eucalyptus* in the Northern Territory" which forms Bulletin No. 17 of the Commonwealth Forestry Bureau; no date appears on this publication, but Dr. Jacobs has kindly informed me that it appeared in 1934. During our work with the N.A.R.S. this was found to be an excellent aid to the identification of eucalypts in the field. Maps showing type localities, figures of characteristic leaves and fruits, original descriptions or their translations (mostly copied from Maiden's "A Critical Revision of the Genus *Eucalyptus*" or Blakely's "A Key to the Eucalypts"), general field characters, and notes on timber, distribution, and similarities all help to make the paper a most useful one from many points of view.

9. Finally, there are the N.A.R.S. collections made by myself in 1946 and 1947 and by R. A. Perry in 1947 and 1948, and the collections made by R. L. Specht during the Commonwealth of Australia—National Geographic Expedition to Arnhem Land in 1948. Perry's collection in 1949 from the neighbourhood of the Victoria and Ord Rivers became available during the final stages of the preparation of this paper. There is much that is of interest amongst these specimens, and material concerning species found in the Northern Territory has been incorporated in this paper; specimens of two species apparently confined to Western Australia are not discussed here.

II. General Considerations and Methods

Scattered through the following pages are to be found several terms commonly met with in the literature of systematic botany. Some of these have been used in differing senses by different authors. For the sake of clarity, their usage in this paper is explained here, together with some conventions used.

1. *Seedling leaves.*—The early leaves on seedlings in their first year, raised from planted seed.

2. *Juvenile leaves.*—(*a*) Leaves of seedlings growing in the wild; these are usually from plants with a well-developed ligno-tuber more than one year old, which are still behaving as seedlings as the result of recent destruction by fire of all above-ground parts; or (*b*) coppice shoots taken from the base or near the base of the tree, or from root-suckers.

3. *Intermediate leaves.*—The large leaves produced after the earlier juvenile foliage and before the adult foliage. Specimens may have been taken from old seedlings that have survived fire for a year or more, or from coppice shoots.

4. *Adult leaves* or *mature leaves.*—The leaves normally produced on undamaged parts in the crown of mature individuals; the terms refer to ontogenetic development, not to physiological development.

5. *Reversion shoots.*—Shoots produced in the crown of the tree, often as the result of some injury, that bear intermediate or even juvenile foliage.

6. *Lateral veins* or *primary lateral veins.*—The veins that diverge from the midrib and continue across the leaf to the intramarginal vein with which they unite at its slight bends or sinuses. In the northern species discussed in this paper, these veins are approximately straight for the greater part of their length. The *angle of venation* is measured as the angle this straight part of the lateral vein makes with the midrib, and refers to the veins in about the middle third only of the leaf. The number of lateral veins on each side of the midrib is approximately the same, and it is convenient to speak of the number of *pairs of lateral veins* to the leaf, although the veins may not leave the midrib opposite one another. The number of pairs of such veins varies for each species within well-defined and often rather narrow limits, provided leaves of similar ontogenetic age are compared. These lateral veins tend to become indistinct towards the apex and here and sometimes elsewhere there may be confusion with the secondary lateral veins. Hence different observers might arrive at a slightly different count of these veins, but counts of one or two above or below those given in this paper will not affect the conclusions to be drawn. Distortion due to accidents during development is common in the leaves of northern eucalypts; this often affects the venation as well as the shape of the leaf, so that well-formed leaves should be carefully looked for, and it is always advisable to check observations on more than one leaf.

7. *Secondary lateral veins.*—The veins sometimes found between successive primary lateral veins, more or less parallel to them, and with which they usually anastomose towards the margin. They rarely reach the intramarginal vein, and when they do, they meet it at a convexity, not at a sinus.

8. *Inflorescence* etc.—The terminology of the inflorescence, bud, and fruit follows that of Blakely, "A Key to the Eucalypts," p. 12. There is a certain margin of error in measuring buds and fruits in those species where the calyx-tube tapers more or less gradually into the pedicel; different observers may arrive at slightly different dimensions.

9. *Collection.*—The piece or pieces gathered by a collector at one time and place which are treated by him as parts of one taxonomic unit and are kept separate from other pieces of the same or different taxonomic units; all pieces are not necessarily taken from one individual.

10. *Number.*—A collection bearing a number attached to it either at the time of gathering by the collector or subsequently by the collector or some other individual.

11. *Specimen.*—The term *specimen* is frequently used to indicate *any* piece of plant material offered or preserved for study. The word may be accompanied by such descriptive words or phrases as "fruiting specimen", "specimen of wood", etc., but it is usually presumed that the "specimen"

is a representative of some individual or specified organ. For systematic studies, it is reasonable to demand that a specimen is an individual that represents the species-population, or a piece or a series of pieces of an individual that is representative of that individual, and this in its turn of the population. If the specimen consists of more than one piece it may be distributed over more than one herbarium sheet. It is now generally recognized that a good specimen of a eucalypt should include juvenile leaves, adult leaves, bark, buds, flowers, and fruit (cf. S. T. Blake in *Aust. J. Sci.* **11:** 121 (1949)). In such cases, where two or more pieces are present, it is common to find in print such phrases as "suite of specimens" or "series (of specimens)", with each piece treated as a specimen.

12. *Duplicate.*—Any specimen of a collection other than the specimen under particular consideration.

13. *Sheet.*—The plant material mounted on a piece of paper with accompanying label, etc., for deposit in the herbarium; or — when specimens are not mounted — the plant material contained in a single folder and segregated from other plant material.

14. *Protologue.*—The printed matter (description etc.) accompanying the original publication of a name or epithet (cf. Wilmott in *J. Bot.* **77:** 206 (1939) in footnote; Furtado in *Gdns' Bull.* **11:** 245 (1941)).

15. *References to specimens.*—The collector's name and number identifies the collection and is used in discussion. When collectors have failed to number their collections, a fault all too common with Australian collectors, the collector's name and the locality are used in identifying the collection. It is frequently desirable to indicate the herbaria in which particular specimens are to be found. In this paper, herbaria are indicated by the following abbreviations which are (with the exception of AFSC) those proposed for international use by Lanjouw in *Chron. Bot.* 5: 142-50:

Queensland Herbarium, Brisbane (herb. Brisbane)	BRI
National Herbarium of New South Wales, Sydney (herb. Sydney)	NSW
National Herbarium of Victoria, Melbourne (herb. Melbourne)	MEL
Australian Forestry School, Canberra	AFSC
Institute de Botanique Systématique de l'Université, Geneva	G
University of Cambridge (Botany School), Cambridge, England	CGE
Herbarium, Royal Botanic Gardens, Kew, England (herb. Kew)	K
British Museum of Natural History, Department of Botany, London	BM
Laboratoire de Phanérogamie du Muséum National d'Histoire Naturelle, Paris (herb. Paris)	P
Naturhistorisches Museum, Vienna (herb. Vienna)	W
Rijksherbarium, Leiden	L
Division of Plant Industry, C.S.I.R.O., Canberra	CANB

The only material from extra-Australian herbaria that I have actually seen is some fragments, photographs, and drawings from Kew and the specimens from Leiden. For other specimens cited, I have relied on published figures.

16. In accordance with some recent trends, all specific epithets are written with a small initial letter*; they are consistently cited in this manner, even if a capital initial letter had been used in any publication referred to. In quotations from Mueller's field labels, an oblique stroke (/) is used to indicate the end of each line of writing.

17. The full synonymy of each species is given, in so far as this has been verified. The original place of publication of each name is given, but no later references. The type of each name is listed, with references to the herbaria in which it has been seen or verified from a photograph or drawing, and to published figures of it. Misidentifications are not listed in the synonymy, but are discussed in the remarks following the descriptions.

18. Limitations on space have restricted the citations of specimens examined to types and other critical specimens, new records, and the N.A.R.S. collections; many of the original observations of the collectors are omitted from the enumerations, but they have been used in drawing up the accounts of the species. Values of latitude and longitude are based on the military maps printed in 1942-44.

III. Types and Nomenclature

According to Art. 18 of the International Rules of Botanical Nomenclature "The application of names of taxonomic groups is determined by means of *nomenclatural types*. A nomenclatural type is that constituent element of a group to which the name of the group is permanently attached, whether as an accepted name or as a synonym. . . . The type . . . of a species or group of lower rank is usually a specimen or preparation . . . . The nomenclatural type is not necessarily the most typical or representative element of a group; it is merely that element with which the name of the group is permanently associated."

The type of a species (or variety) is therefore the specimen from which the author of a name drew up the description that accompanied the original publication of the name. It has frequently happened that the original description was based on more than one specimen, or on specimens from more than one collection, so that there is more than one type. The kinds of types have been discussed in detail by Furtado in *Gdns' Bull.* **9**: 285-309 (1937), but only the terms defined below have been found necessary in this paper.

1. *Holotype.*—The specimen chosen by the author and cited in his original description as that by which the species (or variety etc.) must be interpreted. It is THE TYPE, and is commonly referred to as such.

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* This is now the recommended style; see de Wit in Fl. Males. Bull. No. 7: 223, 231 (1950).

2. *Paratype.*—Any type other than the holotype (when the description was based on more than one specimen).

3. *Syntype.*—Any type, if no holotype was chosen by the author.

4. *Lectotype.*—A syntype selected as holotype subsequent to the publication of the original description.

5. *Clastotype.*—A fragment of a type specimen.

6. *Duplicate types.*—Specimens purported to have been collected by the same collector at the same time and in the same place, and bearing the same number (if any), as the holotype or lectotype. If it is certain that the specimens came from the same plant as the holotype (or lectotype), they may be more critically distinguished as *isotypes;* if it is doubtful that they were collected from the same plant, they may be distinguished as *haptotypes.*

7. *Topotype.*—A specimen from the type locality that agrees with the original description (the *type locality* is the place where the type was collected).

8. *Type collection* is a term used in this paper for a collection that includes a holotype or a lectotype.

9. *Neotype.*—A specimen selected as type when the holotype has been lost.

The term *co-type* has been used to cover all kinds of types except holotype, lectotype, and perhaps topotype. Both type and co-type were very loosely used by Maiden and Blakely.

The species of *Eucalyptus* that have been described with the definite indication of types are relatively few. Some have been described from single collections, and therefore these collections are the type collections. In other cases more than one collection was cited, or only a locality or localities, or the general distribution was stated, often without mention of the name of any collector. The selection of a lectotype then becomes necessary to determine the correct application of the name, and this is often a difficult matter. The Regulations for Determining Types are to form Appendix I of the International Rules of Botanical Nomenclature, but they have not yet been formulated. The following considerations guided the selection of lectotypes cited in this paper:

1. Consideration was given only to those specimens that were available to the author when the description was drawn up.

2. The characters evident on the specimen must in no way disagree with the description, although characters may be described that are not to be found on a particular specimen (owing to damage, removal of clastotypes, etc., or to the existence of syntypes).

3. In the species described by Mueller in his paper of 1859, any notes on bark etc. on field labels are treated as "characters on the specimen", since Mueller definitely stated that his descriptions were drawn up in the field.

4. Other things being equal, the specimen preserved in the herbarium with which the author was most closely associated is preferred as lectotype.

5. Some of the types of Mueller's names collected during the Gregory Expedition may be at Kew, because Mueller sent all or the best part of some collections to that institution.

6. For reasons given above, specimens collected by R. Brown and Bauer are regarded as equivalent for the typification of names.

7. In a map accompanying his paper, Jacobs has marked by means of numbers the "type localities" of all species described from the Northern Territory. According to the explanation on p. 36, "The figures in squares refer to the first-mentioned and most reliable typical locality for species of which a single type locality is not given in the original descriptions." "If this is to be interpreted as a deliberate choosing of a lectotype locality, and consequently as an indirect selection of a lectotype, then complications arise, even though it may be safely presumed that the localities are often intended to be approximate only (such as those represented by the cluster of numbers about Pine Creek and Burrundie). For instance, *E. grandifolia* R. Br. ex Benth. was founded entirely upon Brown's specimens from Islands of the Gulf of Carpentaria, and it is misleading to have Stapleton marked as "the first-mentioned and most reliable typical locality" for the species. *E. pyrophora* Benth. was described from specimens from the Victoria River and from Western Australia; Maiden typified the name on the Victoria River specimens, yet a locality on the Roper River is marked on the map as "the first-mentioned . . . locality." Further, localities marked "type localities" for species described by Blakely and Jacobs do not always agree with those of specimens marked "type" in the Sydney Herbarium. For these reasons, the choice of lectotypes has not been greatly influenced by the map.

8. Maiden and Blakely appear to have had a rather vague concept of nomenclatural types, and some specimens marked "type" and "co-type" in the Sydney Herbarium are not those used by the author in drawing up the original description of the species concerned. In his published works also, Maiden has quoted as "types" some specimens which were collected many years after the species were described.

9. A lectotype has not been chosen in every case where the interpretation of the name rests upon two or more syntypes. A definite choice has been avoided when the application of the name has not been in doubt and the specimens appear to represent the same taxonomic unit. If any other worker has grounds for restricting the use of the name, the way is still open for him to make a choice in accord with his evidence.

All references to rules of nomenclature are to "International Rules of Botanical Nomenclature", 3rd Ed. (1935) and Supplement (1948).

The unofficial version compiled by Camp, Rickett, and Weatherby for the American Society of Plant Taxonomists and published in *Brittonia* **6**: 1-120 (1947) and reissued by The Chronica Botanica Co. (1948) differs from the official version (the Supplement) in some passages, but these differences do not affect any reference in this paper.

IV. The Genus and its Major Groups

The chief character distinguishing *Eucalyptus* from other capsular-fruited genera of the Myrtaceae is that the perianth is represented in the bud by a lid-like operculum, which is cast off in its entirety when the flower expands. Frequently two opercula are present, an outer one, which is usually shed from the very young bud and probably represents the calyx, and an inner one representing the petals. Possibly in some groups the operculum may consist of both calyx and corolla.

The genus has usually been regarded as a natural one, and very few proposals have been made to treat any groups within it as distinct genera. Mention may be made of *Eudesmia* R. Br. and *Symphyomyrtus* Schau.; both were founded on single species, the former with the stamens arranged in four groups, the latter with the flowers and fruits more or less immersed in the swollen apex of the peduncle. In a lengthy paper on the development of the family in *Trans. Linn. Soc. N.S.W.* 38: 529-68 (1913), C. E. Andrews proposed that several groups should be treated as distinct genera and suggested names for them; neither the method of publication nor the formation of the names is in accord with the International Rules of Botanical Nomenclature, and Andrews himself made no transfers but continued to refer to the species under *Eucalyptus*.

Eucalyptus has been more extensively and intensively studied than any other group of Australian plants. The genus is a large one with over 600 species and varieties, according to Blakely, and like all large genera, it presents many difficulties to the taxonomist. But there appears to be no sound reason for regarding it as more difficult, or less amenable to orthodox taxonomic treatment, than such genera as *Melaleuca, Acacia, Panicum, Andropogon* and its allies, *Aristida, Cyperus, Rubus,* etc. Some of the difficulties encountered are the direct result of the way in which many species have been described and classified. As the result of its early cultivation in Europe, numerous species have been based on juvenile plants or otherwise very unsatisfactory material with hopelessly inadequate descriptions published sometimes in garden catalogues, trade catalogues, etc. Individuals of the genus are so nearly ubiquitous in Australia that nearly every resident and visitor must have seen at least one individual. By the variety of their barks, the usefulness and variety of their timbers, and the presence of gums and kinos and of essential oils — and also, perhaps, because of their ubiquity — species of the genus have received attention from a wide variety of observers besides botanists, including engineers, chemists, geologists, entomologists, and ordinary travellers, and some of these have not hesitated to publish opinions on the classification of the genus and the limits of its species in a wide variety of publications that are often relatively inaccessible to the average botanical public, and include daily newspapers, geographical, geological, and zoological journals, and works of primarily a chemical nature. We now have classifications based on barks, on timber, on the essential oils, on kinos, on buds, on anthers, on fruits, on seeds, on the position, shape, and venation of the leaves, and on the anatomy of the petiole. Some of these classifications appear more like classifications of plant products than classifications of the plants producing them; most of these attempts have been discussed or quoted by Maiden in various parts of his "A Critical Revision of the Genus *Eucalyptus*".

It is now traditional that the species of *Eucalyptus* are highly variable. On the other hand, R. T. Baker, in *Rep. Aust. Ass. Advanc. Sci.* 1900: 229-30 (1901) claimed "that much of the hitherto supposed variability of specific characters of our Eucalyptus trees is the result of various artificial classifications applied to the species in the past, whereas, if classified on what appears to be a natural basis, the species possess very little, if any, variability . . ." In his elaboration of this statement, he claims that classifications based on morphological characters are artificial, and that "By following a natural classification, that is, one founded on a long and intimate acquaintance with the trees in nature, their habits and places of growth, the form and qualities of their seed, the manner of their elevation, increase and reproduction, the peculiarities of their radication, their interior substances, the infinitely varied formation of their vascular system . . . , the peculiar qualities of seeds, salts, gums, resins, oils by which they are distinguished, and all other constituents on which their natural combination so ultimately depends, almost all traces of variability disappear . . ." It is not clear just what Baker meant by "morphological characters", but the purpose of his paper appears to be a demand that eucalypts should be studied as organisms, not merely as dried fragments in a herbarium.

Most of the generalizations on the genus have been based on species in the southern parts of the continent; I am not well acquainted with these, but so far as my experience with the species of the northern parts is concerned, the genus closely resembles many others in the problems it presents to the taxonomist and plant geographer. There are many well-marked species upon the reality and limits of which there has been little or no question; examples are *E. miniata, E. phoenicea, E. tetrodonta, E. ptychocarpa,* and *E. curtisii.* This is not to say that any specimen exactly matches any other specimen of the species, because it may not; individual variation occurs in these as in other species, but it is relatively slight. Next there are series of closely similar forms, the differences between which are definite and sharp but difficult to express in words; *E. clavigera* and its allies form such a series, which is discussed in some detail in this paper. These forms are treated by some as distinct species, by others as varieties of variable species, with the treatment depending partly on the experience of the worker and the quality and range of the material available to him, partly on his attitude to "specific differences" and "varietal differences"; the areas of distribution of these forms may coincide to a more or less degree, or they may overlap, or they may be quite distinct. Then there are those complex groups of forms of which the extremes are relatively quite distinct, but between these extremes there are found apparently continuous series of intermediates. These are the groups that cause such trouble to the taxonomist, and at times they appear to defy any attempt at classification; they appear to be relatively numerous in *Eucalyptus*. Sometimes the difficulties prove to be more apparent than real, owing to insufficient herbarium material or to the fact that this material is badly selected, imperfect, or otherwise not representative; in these cases the difficulties gradually disappear as experience in the group grows and more evidence accumulates. Many named groups are still represented in herbaria by quite inadequate material. The possibility of hybrids adds to the difficulties in the herbarium; collectors naturally collect that which appears "different" and sometimes the unusual is represented by as much material as the usual, which may be neglected because it is common or presumed to be well known. When the systematist is also the collector, the amount of time available often handicaps his efforts.

The study of the tropical eucalypts is beset with difficulties that are not encountered in the more southern parts of the continent. Many species have large leaves, which makes the adequate representation of the individual by a single piece an impossibility, particularly so where large inflorescences are also produced; more time, care, and space are required to collect representative material. Further, many species are partly or wholly deciduous during at least part of the dry season, so that adequate material is not always to hand anyway, while the new leaves produced towards the end of the dry season may give a wrong impression of the nature of the mature leaves. A third difficulty, and a very serious one too, is that trees commonly produce flowering shoots bearing leaves of the "juvenile" or "intermediate" form (reversion shoots). Particularly on smaller trees (up to about 6 or 7 m. in height) this may be the result of the fires that commonly sweep the country during the dry season, but it seems that this is not the only factor, for leaves of "intermediate" form have been found on tall trees. It may be remarked that such "reversion shoots" are most noticeable on trees that are commonly deciduous. Specimens consisting of such reversion shoots, studied without reference to the normal adult leaves (which may or may not be present on the same trees) are sure to lead to confusion. This phenomenon is distinct from that of young trees flowering while still in the "juvenile" state. *E. foelscheana* is mentioned in the original description as flowering when only 18 in. high, and I have seen it behaving in the same way.

There are very few references to deciduous leaves in *Eucalyptus*, and all species have been tacitly supposed to be evergreen. Maiden (Crit. Rev. *Eucalyptus* **6**: 417 (1922)) stated that "It is unusual for a Eucalypt to be deciduous, and it is only the case with some tropical species, *e.g., E. alba* (*platyphylla*) . . . *E. Houseana* . . . is also deciduous in some seasons." Kessell and Gardner (Key Eucalypts W. Aust. 29 (1924)) stated that *E. brachyandra* "is deciduous, being almost or entirely leafless in the dry months." In a modified form, this statement was repeated by Blakely (Key Eucalypts 221) and (on p. 139) he quoted Jensen as stating that *E. bigalerita* (*E. pastoralis*) sheds its leaves in the dry season; no mention of deciduous leaves occurs in the generic description (pp. 5-6).

Several other species are more or less completely deciduous. I have observed trees of the following species to shed all or nearly all their leaves during part of the dry season (cf. Plate 1; Plate 2, Fig. 3): *E. alba, E. apodophylla, E. bigalerita, E. confertiflora, E. foelscheana, E. grandifolia, E. latifolia, E. oligantha, E. staigeriana* (a species of northern Queensland), and *E. tectifica;* some other species, such as *E. jensenii,* are at least partly deciduous. The degree of completeness of leaf-fall and the period between fall and new growth appear to depend partly on local conditions.

These vagaries in flowering, in the production of "intermediate" leaves among the adult ones, and the more conspicuous variation in size and shape of adult leaves of large-leaved species all tend to emphasize the "variability" commonly accepted as one of the characteristics of species of this genus. It is possible that the emphasis on variability has been sometimes misplaced, for it has appeared to me that in many instances the range of variability between different parts of the same individual may be but little less than the supposed variability of the species.

Species, as used in this paper, may be approximately defined as populations between any two of which there is a tangible discontinuity in morphological characters; the populations may be continuous or discontinuous in space. That is, the sharpness of the difference (not its amount or kind) is the important feature, and species may have a continuous or strongly discontinuous distribution.

The term "form" is used rather freely in this paper to denote individuals or a group of individuals more or less exactly agreeing in morphological characters with a particular specimen under discussion; this specimen may, or may not be the type of some name. The term is merely one of convenience in discussions; it has no taxonomic significance as to rank and may refer to a species, to some segment of a species, or to individuals, or to portions of an individual. No attempt has been made to discriminate by name subspecies, varieties, or other infra-specific groups. The terms *subspecies* and *variety* are sometimes synonymous, but the former does not appear to have been used in any work on *Eucalyptus*. They are used in a diversity of senses. By some workers they are used to designate forms distinguishable from the typical form of the species, but between which intermediates are known or suspected to occur. By others, subspecies, varieties, and other categories are used to classify forms (in the sense used in this paper) according to the amount of difference between them and the typical form of the species; the amount of difference observable commonly depends on the selection of specimens available to the worker, and the rank (and therefore the name) assigned to any form is thus often tentative in the extreme. A use of the term subspecies (or variety) that is growing in popularity is to denote a geographical race (a segment of a species-population isolated in space from the segment represented by the type specimen and differing from it more or less in morphological characters); any permanent value of the terms in this sense demands a knowledge of the geographical range of the species and the amount of individual variation.

So far as *Eucalyptus* is concerned, the idea of extreme variability is so generally accepted that little is gained (except, perhaps, in theoretical discussions) by the formal recognition of named varieties in the first sense, while much is lost in clarity and brevity by the use of a ternary nomenclature. A classification based on the degree of difference at length results in the polycategorical nomenclature favoured by some (chiefly European) botanists, a type of nomenclature from which *Eucalyptus* is happily free (so far), though a number of varieties have been proposed on characters which were said to be insufficient to distinguish species. If "discontinuity" (sharpness of difference) had been the criterion instead of amount of difference the reasons for proposing many of these varieties would disappear. At least in most species, too little is yet known about the correlation (if any) between variation and geographical distribution to warrant the idea of geographical races being expressed in nomenclature, although it may be very useful in studying the morphological limits of a species. It may well be that this method of approach would do much to solve some of the problems of classification in the genus.

Hybridization between species is believed to occur and some examples of suspected hybrids are cited in this paper. The suspicion of hybridism rests upon the fact that in communities containing a large number of individuals of two (or more) readily distinguishable species there is occasionally found a tree, a few isolated trees, or a small group of trees that exhibit characters of, or intermediate between, both the suspected parent species and are not sharply distinguished from either. This criterion presupposes a fairly extensive acquaintance in the field with the species concerned.

V. SUBDIVISIONS OF THE GENUS

Many attempts have been made to arrange the species in sections, subsections, series, and subseries, but the nomenclature of these groups is very complicated, and no serious attempt has been made to unravel it in this paper. Often no rank was assigned to the groups indicated, and usually groups distinguished on one basis of classification were named (if at all) independently of groups named in earlier classifications. Maiden, for example, proposed several classifications based on individual characters (seed, bark, leaf venation, anthers, etc.), and he gave formal names to some groups. In some cases, as in that of leaf venation, the classification resembles a classification of the variation in certain morphological characters rather than a classification of species possessing these characters; names proposed in these cases may well be neglected in nomenclatural considerations. It will be a major nomenclatural task to investigate the correct names for the numerous subdivisions of varying rank defined by Blakely; certainly some names were chosen contrary to the International Rules of Botanical Nomenclature (e.g. *Tessellatae*, discussed later in this paper), and others were wrongly formed, such as *Corymbosae* (*Non-Peltatae*).

For convenience in the enumeration of the species and in discussion, the species dealt with in this paper are arranged in Series. These series are much the same as those recognized by Blakely; one important exception is discussed later. These groups afford an arrangement sufficiently convenient for the purposes of this paper, while most nomenclatural problems of the intra-generic groups can be avoided.

Furtado (*Gdns' Bull.* **12**: 318-9 (1949)) has pointed out that orthodox practice is to accord priority to the names of such groups as sections and series only when the basis of classification remains similar, and has suggested on pp. 319 and 374 that Art. 53 of the International Rules of Nomenclature should be modified to accord with this practice. Such a procedure would certainly greatly reduce the problems of infra-generic nomenclature in *Eucalyptus*.

VI. Taxonomy and Enumeration of Species

The order in which the species are dealt with differs in places from the arrangement adopted by Blakely. This rearrangement is purely one of convenience for the purpose of this paper; it is not a commentary on Blakely's arrangement and it is not intended to have any phylogenetic significance.

Series Eudesmiae (Benth.) Blakely

1. **Eucalyptus odontocarpa** F. Muell. in J. Linn. Soc. (Bot.) 3: 98 (1859)

Shrub, mostly 1.2-2.5 m. high, but up to 3 m. high according to Mueller, with several slender stems and smooth, pale grey to whitish or brownish bark, deciduous in brownish flakes; twigs slender, more or less angular. Juvenile leaves opposite for many pairs, sessile and rounded at the base to more or less connate, oval to lanceolate. Intermediate leaves opposite and connate, narrowly ovate to broadly lanceolate, more or less obtuse, up to 8 × 4.5 cm. Adult leaves more or less opposite to distinctly alternate, prominently petiolate, concolorous, shining green when fresh but dull and more or less yellowish green when dry, linear-lanceolate, 7-12 cm. long, 0.6-1.5 cm. wide, about 6-15 times as long as wide, prominently veined with the intramarginal vein up to 1 mm. or more distant from the edge and about 20-30 pairs of lateral veins at an angle of 20°-30° with the midrib; petioles up to 1.6 cm. long. Flowers axillary and terminal, in pedunculate, solitary or paired, 2-3-flowered umbels or sometimes solitary; peduncle up to about 5 mm. long; pedicels up to 3 mm. long, slender. Buds turbinate, not sharply marked off from the pedicel, between 4 and 5 mm. long and between 3 and 4 mm. wide; calyx-tube more or less 4-angled, the angles at the top more or less produced into short, blunt, erect or more or less spreading teeth; operculum about one-third as long as the calyx-tube, almost patelliform, muticous. Stamens in a continuous series; anthers very small, versatile, more or less oblong, with parallel cells opening in longitudinal slits. Fruit sessile or subsessile, subcylindrical and narrowed to the base or somewhat turbinate, more or less tetragonous with 4 small or rudimentary teeth at or just below the narrow rim, 8-12 mm. long, 5-6 mm. wide, with 3 enclosed valves. Seeds obliquely ovate or oblong, irregularly triquetrous, the ventral side concave with the hilum about the middle, the dorsal side convex to acutely keeled, rugose and shining, 3.5-5 mm. long and 2-3 mm. wide, with acute edges surrounded by a narrow, scarious wing.

WESTERN AUSTRALIA.—Twenty miles S. of Nicholson Station, on skeletal soil with *E. brevifolia* and *Triodia pungens*, 6.vii.1949, *Perry* 2372. NORTHERN TERRITORY.—Helen Springs, 29.vi.1947, *Perry* 139; near (S. of) "Banka Banka", forming open scrub with *Triodia* sp., 2.xi.1946, *Blake* 17364; 10 miles NW. of Tennant Creek, shallow, stony soil, 25.iv.1948, *Perry* 587; W. to SW. of Soudan Station, 20° 5′ S., 136° 50′ E., with *Triodia pungens* on stony ridge, hard red soil, alt. about 225 m., 16.vi.1946, *Blake* 15970. QUEENSLAND.—Burke District: On Barkly Downs Station, 20° 22′ S., 138° 25′ E., in open scrub of chiefly *Acacia* and *Triodia* on red, stony soil, 238 m., 27.v.1947, *Blake* 17945.

Type.—Sturt Creek, Feb. 1856, *F. Mueller* (MEL, K); drawing from specimen at Kew reproduced in Maiden, Crit. Rev. *Eucalyptus* 5: Plate 186, Figure 1.

Widely spread and locally dominant in the desert scrub in the region of the 15-in. isohyet in the Northern Territory, extending into Western Australia on the one hand and just over the Queensland border on the other (map 17*B*). It is readily distinguished by its mallee form and the four teeth on the calyx-tube; these may be very prominent indeed as in *Blake* 17364, or they may be obscure as in the other specimens cited.

The connate intermediate leaves seem not to have been previously described. There are many intermediate leaves on some of the fruiting specimens of *Blake* 15970 which thus have a very heterophyllous appearance; the leaves vary in width from 42 mm. down to 6.5 mm. in the extreme adult state. The four angles on the calyx-tube ending in small teeth are quite evident on the bud and flower, but the angles and sometimes also the teeth tend to disappear from the fruit.

2. **Eucalyptus tetrodonta** F. Muell. in J. Linn. Soc. (Bot.) 3: 97 (1859)

An evergreen, usually straight tree mostly 10-24 m. high with grey, long-fibrous, compact, persistent bark throughout. Juvenile leaves opposite for many pairs, petiolate, oblong-lanceolate, more or less obtuse, glabrous, with about 7 pairs of lateral veins. Intermediate leaves opposite, broadly lanceolate, large, up to 20 × 7 cm. or more. Adult leaves alternate or also opposite, prominently petiolate (petioles 1-2 cm. long), falcate-lanceolate, acute or acuminate, about 10-20 cm. long and 1.5-4 cm. wide, about 5-10 times as long as wide, concolorous and dull, with about 25-30 pairs of somewhat irregular lateral veins at an angle of 45°-50° with the midrib. Inflorescences of axillary and apparently terminal, pedunculate, 3-flowered umbels or reduced cymes; pedicels flattened, broadened upwards, 6-10 mm. long. Buds obovoid or somewhat pyriform, 10-12 mm. long and 8-10 mm. wide; calyx-tube somewhat campanulate, more or less distinctly 4-angled, commonly with 4 teeth or rounded lobes at the top; operculum about as long as the calyx-tube, more or less hemispherical, with 8 faint to prominent ribs, which are sometimes somewhat winged, sometimes quite obscure. Anthers oblong, versatile, with a dorsal gland and parallel cells opening in longitudinal slits. Fruit sessile or shortly pedicellate, cup-shaped to subcampanulate, more or less distinctly 4-ribbed, particularly near the base, with 4 rounded lobes shortly below the narrow rim, about 1.3-1.7 cm. long and 1.0-1.2 cm. wide; disc lining the interior of the calyx-tube; valves 3, enclosed to about flush with the rim.

NORTHERN TERRITORY.—About SE. of Brocks Creek, 13° 37′ S., 131° 33′ E., dominating open forest on sandy soil, about 150 m., 6.vii.1946, *Blake* 16343.

Type.—Entrance of the Victoria River on dry cliffs, Sept. 1855, *F. Mueller* (MEL); Plate 9.

Widely spread over northern Australia (map 17*A*), chiefly on sandy soil. It may be locally dominant, but it is frequently co-dominant with *E. miniata.* It is commonly known as "messmate" or "stringybark".

The four prominent teeth on the relatively large buds and fruits readily distinguish this species in the herbarium, and in the field it is equally distinctive by reason of the long-fibrous bark and the pendulous and prominently falcate, rather large leaves.

Two broad bracts are conspicuous in young inflorescences, and in this stage, the lobes of the calyx-tube quite resemble four thick sepals.

Series MINIATAE Blakely

3. **Eucalyptus phoenicea** F. Muell. in J. Linn. Soc. (Bot.) 3: 91 (1859)

Usually a slender tree, up to about 10 m. high, with thick, yellowish, thinly fibrous-flaky bark on at least the greater part of the trunk and cream or white, smooth bark on at least the upper branches and there deciduous in small scales. Juvenile leaves opposite for many pairs, subsessile, suborbicular to ovate, more or less cordate, broadly rounded to slightly emarginate at the apex, from about 3 cm. long and wide up to 5 cm. long and 3.8 cm. wide, with 5-8 pairs of lateral veins, slightly paler beneath, sparsely scabrous-pubescent with stellate hairs becoming more or less tomentose on the midrib beneath, petioles, and stem. Adult leaves glabrous, alternate, petiolate, about the same colour on both sides, lanceolate, straight or falcate, acute or acuminate, tapering to a petiole 0.8-1.5 cm. long, mostly 8-12 cm. long and 1.5-2.3 cm. wide, about 3.5-6 times as long as wide, with about 20-36 pairs of somewhat irregular primary lateral veins at an angle of 50°-65° with the midrib. Inflorescences in the axils of fallen leaves, of solitary (sometimes opposite), pedunculate, many-flowered umbels; peduncles relatively slender, about 2-2.5 cm. long; pedicels relatively slender, about half as long as the calyx-tube in flower, up to about 5 mm. long in fruit. Buds very narrowly pyriform, rather sharply distinct from the pedicels, 1.2-1.8 cm. long and 0.5-0.7 cm. wide; calyx-tube more or less funnel-shaped, produced for a considerable distance above the ovary and there slightly expanded, indistinctly ribbed; operculum obtusely conoid, about half as long as the calyx-tube. Anthers versatile, oblong, with a dorsal gland and parallel cells opening in longitudinal slits; filaments orange-yellow to scarlet. Fruit subcylindrical, rounded at the base, abruptly narrowed for a short distance below the rather thin and sometimes spreading rim, several-ribbed, 2.5-3 cm. long and 1.1-1.2 cm. wide, with 2 or rarely 3 very deeply enclosed valves. Seeds ovate, somewhat concavo-convex with rounded edges and no wing, irregularly rugose, about 4 mm. long and 2.5-3 mm. wide, with the hilum on the concave surface.

NORTHERN TERRITORY.—Between Blackfellow Creek and Reynolds R., 13° 30′-32′ S., 130° 47′-54′ E., associated with *E. miniata* in open forest on stony gentle slope, 113 m., 31.vii.1946, *Blake* 16683; 30 miles N. of Katherine, near Edith R., sandy soil on granite, 28.viii.1948, *Perry* 1937.

Syntypes.—"Victoria River, near the Main Camp" (i.e. about 15° 35′ S. and 130° 25′ E.), May 1856, *F. Mueller* (MEL, BRI); and "Ranges near the Fitzmaurice River", Oct. 1855, *F. Mueller* (MEL).

Rather widely distributed through the northern part of the Northern Territory, chiefly on stony hills with shallow, sandy soil. Sometimes it occurs alone, but frequently it is associated with *E. miniata* or *E. dichromophloia* (map 18*B*).

Juvenile leaves and seeds of this species have not previously been described. Blakely's account in Key Eucalypts 72, of the bark and habitat is not in accord with the observations of Mueller, Jacobs, or myself. His record of the species from Queensland and the vernacular name "ngainggar" is based on *Roth* 287 from Cape Bedford, but the material is too scrappy for certain identification, and the locality far distant from other known localities for the species.

The species is closely allied to *E. miniata,* and often resembles it very closely, but it is commonly a smaller tree with the rough bark often extending to the branches and more yellowish in colour, with usually narrower leaves not distinctly paler on the lower surface, more numerous and more slender flowers on longer and slender pedicels, and narrower, smaller, less distinctly ribbed, usually 2-valved fruits. The filaments are said to vary from crimson through scarlet to orange; they were orange-yellow on the only tree I have seen in flower, but they became more reddish when dried.

The figure in "Eucalyptographia", dec. 1, appears to have been drawn from Mueller's specimen from the Victoria River (the first syntype mentioned above), and the fruits figured in Maiden, Crit. Rev. *Eucalyptus* 3: Plate 96, Figure 8, may have come from the same specimen; there is now no fruit on the specimen.

4. **Eucalyptus miniata** A. Cunn. ex Schau. in Walp. Repert. 2: 925 (1843)

E. aurantiaca F. Muell. in J. Linn. Soc. (Bot.) 3: 91 (1859).

Tree, usually straight and tall, up to 30 m. high; bark on lower or greater part of trunk grey to somewhat yellowish, thick, fissured, spongy-papery, removable in thin scales; remainder with smooth, white or whitish bark shedding in papery flakes; smaller branches sometimes pruinose; twigs angular. Juvenile leaves opposite for many (up to at least 8) pairs, prominently petiolate, broadly elliptic-ovate to oblong-lanceolate, obtusely rounded to somewhat emarginate, more or less apiculate, more or less abruptly rounded to somewhat cordate at the base, distinctly 3-nerved in the early leaves and these with as few as 6 pairs of lateral veins, closely stellately hairy on both sides and also more or less tomentose on the lower surface on the midrib (at least) and on the petioles and stems. Intermediate leaves more or less alternate, becoming glabrous, ovate or ovate-lanceolate, and larger than the adult leaves. Adult leaves alternate, oblong-lanceolate, straight or somewhat falcate, sometimes slightly oblique at the base and there narrowed to a petiole of 1.5-1.8 cm., acute or shortly and sometimes abruptly acutely acuminate, mostly 9-13.5 cm. long and 2-4 cm. wide, 2.5-6 times as long as wide, with 22-30 pairs of lateral veins at an angle of 45°-65° with the midrib. Flowers in axillary umbels mostly on the older wood below the leaves; peduncles very stout, about 2-3 cm. long, up to 8 mm. thick. Buds glaucous, rather narrowly pyriform, on short (up to 5 mm. long) and thick pedicels, with 8-10 conspicuous ribs, 1.5-1.8 cm. long and 0.8-1 cm. wide; operculum ovoid-conical, about half as long as the calyx-tube; calyx-tube produced well beyond the top of the ovary. Anthers versatile, oblong, with a dorsal gland and parallel cells opening throughout in longitudinal slits; filaments scarlet or orange. Fruit ovoid-urceolate or more or less barrel-shaped, coarse and woody, with 8 prominent ribs and sometimes fainter ones between, from 3 cm. long and 2.3 cm. wide up to 7 cm. long and 5 cm. wide; valves 3 or 4, deeply enclosed.

NORTHERN TERRITORY.—S. of Brocks Creek, alt. 67 m., common and often co-dominant in *Eucalyptus* forest on usually more or less sandy soils, 29.vi.1946, *Blake* 16220; 18 miles E. of Borroloola, sandy upland laterite with *E. tetrodonta*, 13.vii.1948, *Perry* 1853; 6 miles N. of Woologorang Station, igneous hill with *Eucalyptus dichromophloia*, 2.vi.1948, *Perry* 1183.

Types.—Of *E. miniata*: *Cunningham* 241/1820 from York Sound, Western Australia; not seen.

Of *E. aurantiaca*: "Tableland 26.7.56," *F. Mueller* (MEL); at this date, Mueller was near the Cox R., about E. of the present homestead of "Nutwood Downs".

Widely spread throughout northern Australia, from the Kimberley Division of Western Australia to northern Queensland (map 18*A*), occurring either alone or more commonly in association with *E. tetrodonta* and sometimes also in association with other species. It is commonly known as "woolly-butt", in allusion to its characteristic bark. It is an evergreen tree with the leaves turning more or less russet before they fall; over a large part of the year a few russet leaves can usually be seen on any particular tree.

The very glaucous, strongly ribbed buds borne in umbels below the leaves, the scarlet to orange filaments, the large, woody, longitudinally strongly ribbed fruits with deeply enclosed valves, and the peculiar bark are a very characteristic combination of characters. The fruits frequently resemble those of *E. ptychocarpa*, but the latter have 4 or 5 valves and slender pedicels and are borne in terminal corymbose panicles.

The description of the juvenile and intermediate leaves has been drawn up from *Blake* 12451 from Croydon, Queensland, and differs from that given by Blakely, Key Eucalypts 73 ("opposite for 3-4 pairs, cordate, elliptical to broadly lanceolate, petiolate, minutely stellate, 6-12 × 7-9 cm."), but is more in accord with the description of seedlings in Maiden, Crit. Rev. *Eucalyptus* 8: 138. The more numerous opposite leaves in my collection vary from 2.3 × 2.1 cm. up to 8 × 3.3 cm., and so are much smaller than those described by Blakely, but a good gradation to alternate leaves is not shown. Blakely's description appears to have been taken from the specimens collected by G. F. Hill, which were discussed and figured by Maiden (5: 198 and Plate 193, Fig. 3). From Maiden's figures and remarks it seems possible that Hill's material came from vigorous coppice shoots, which could account for the few pairs and large leaves.

Although I have not seen any part of the type collection of *E. miniata*, I have no doubt that this name has always been correctly applied. The specimens seen by Schauer appear to have rather wider leaves than usual; otherwise his description fully agrees with the species as generally understood. At Sydney, there is a specimen collected by Cunningham on Greville Island with leaves smaller and narrower than those described by Schauer, and this is quite characteristic of the species. There is no date on the label, but Greville Island (which is near York Sound) was not visited until

1821 (P. P. King, Narrative of a Survey of the Intertropical and Western Coasts of Australia . . . 2: 53 (1827)); the type was collected in 1820. Maiden's statement (3: 43 (1914)) that his Plate 95, Figure 3 was drawn "from the type, collected by Ferdinand Bauer" is obviously erroneous. The type of *E. aurantiaca* is very scrappy, but is certainly conspecific.

Series CLAVIGERAE (Maiden) S. T. Blake

The seven species included here form a well-defined group characterized as follows:

Inflorescences predominantly axillary, sometimes on leafless branches and then apparently terminal (Plate 2, Fig. 1, and Plate 11); flowers few to several, in small cymose panicles frequently reduced to simple or compound umbelliform clusters; when leafless,the flowering branches resemble terminal, elongated, more or less cylindrical, often densely flowered, thyrsoid panicles. Buds pyriform with slender pedicels. Operculum thin, more or less patelliform, pallid, sharply circumsciss. Flowers with the free part of calyx-tube more or less saucer-shaped and very much wider than the ovary. Stamens all perfect; anthers versatile, oblong or obovate-oblong with parallel cells opening throughout in longitudinal slits, and with a large dorsal gland. Fruits fragile with very thin walls, truncate-ovoid or cup-shaped to slightly urceolate or campanulate, with usually 3 completely and usually deeply enclosed valves. Seeds more or less rounded or ovate in outline, thin and more or less concavo-convex, with the hilum on the concave surface, with blunt and unwinged to acute or marginate edges. Juvenile leaves opposite for many pairs, never peltate, with as few as 5 pairs of lateral veins. Adult leaves sometimes very different from the juvenile leaves, opposite or alternate, sessile to prominently petiolate, horizontal or vertical, concolorous; lateral veins in about 10-70 pairs, at an angle of 40°-80° with the midrib, sometimes irregular; intramarginal vein close to or remote from the margin, sometimes irregular and sometimes double. Trees of varied habit, sometimes shrubby; some species are deciduous during the dry season. Bark, at least on the upper part, smooth, white or pale grey, deciduous, sometimes grey-scaly towards the base, or the lower part with persistent, dark grey, closely and evenly tessellated bark (Plate 2, Fig. 1; Plate 3, Fig. 2; Plate 4, Fig. 1; Plate 5, Fig. 2).

Blakely referred the *Clavigerae* to Series *Corymbosae* (*Non-Peltatae*); *E. tessellaris*, *E. papuana*, and *E. grandifolia* constitute his subseries *Tessellatae*, while the other forms were surprisingly placed in subseries *Setosae* with the very different *E. setosa*, *E. ferruginea*, and *E. abbreviata*. At least two earlier names have been proposed for the group. Maiden, op. cit. 4: 184 (1919), suggested the use of the name *Angophoroideae* for *E. clavigera* and its allies, but no rank was assigned to the group and no description seems to have been published. Later, op. cit. 6: 525, 535 (1923), he characterized a group that he called *Clavigerae* to which he referred

E. aspera, E. clavigera, E. grandifolia, and *E. tessellaris.* The rank of this group is not expressly stated, but from an examination of the general treatment, it appears to be a subseries. So far as investigations have proceeded, *Clavigerae* appears to be the correct name for the group as a subseries.

Because of its distinctiveness, I have treated the group as a series. The name *Clavigerae* is taken up, because it is the earliest name applied to the group that has been accompanied by any sort of descriptive phrase. The *Clavigerae* differ from the *Corymbosae* as follows:

Inflorescence axillary, not terminal; operculum thin and neatly circumsciss, not thick and irregularly or imperfectly circumsciss*; flower with free part of calyx-tube saucer-shaped and much wider than the ovary, not more or less tubular; ovary commonly 3-celled, not 4- or 5-celled; fruit with very thin walls and soon falling, not thick-walled and long-persistent; seeds concavo-convex without terminal wings, not biconvex and frequently with terminal wings; and the venation of the adult leaves less regular, with fewer lateral veins.

5. **Eucalyptus clavigera** A. Cunn. ex Schau. in Walp. Repert. 2: 926 (1843)

E. polysciada F. Muell. in J. Linn. Soc. (Bot.) 3: 98 (1859).

A more or less crooked and scraggy tree usually 2.5-6 m. high, rarely more and sometimes less, with rigid, spreading, brittle twigs; wood brown when freshly cut. Bark on lower or greater part of trunk persistent, grey, closely and evenly tessellately fissured, elsewhere smooth, pale grey to whitish, deciduous in long flakes. Juvenile leaves ovate, acute, not peltate, subtruncate at the base, flat, prominently petiolate, opposite for at least 8 pairs, at first minutely and sparsely setulose on the petiole and the lower surface of the basal part of the midrib but the blade soon becoming quite glabrous, mostly from about 6 × 4 cm. up to 9 × 5 cm., with about 12-15 pairs of primary lateral veins, prominently reticulate, the intramarginal vein close to the edge; stem more or less terete, sparsely and minutely setulose. Intermediate leaves glabrous, ovate, acute, more or less falcate, stoutly petiolate, up to 33 × 17.5 cm. Mature leaves prominently petiolate, opposite and alternate, ovate or ovate-oblong to oblong-lanceolate or lanceolate, mostly 1.7-4 (rarely up to 6) times as long as wide, obtuse or acute, rounded to subtruncate or more or less broadly cuneate at the base, straight or somewhat oblique or falcate, flat at the margins, concolorous, entirely glabrous, mostly from 9 × 4 cm. up to 20 × 3.5 cm.; veins mostly prominent, the intramarginal vein well removed from the margin in the broader leaves, closer to it in the narrower ones, the primary lateral veins in about 18-25 pairs at an angle of 45°-70° with the midrib; petioles 0.8-2 cm. long, rarely so short as 0.4 cm. Inflorescences quite glabrous, of subsessile to shortly and corymbosely paniculate, axillary, simple or compound, several-flowered umbels, often on leafless branches, so that an apparently terminal, compound, spike-like panicle is produced; pedicels very slender, longer than the buds, mostly 1-2 (rarely only 0.8) cm. long. Buds glabrous, pyriform, 6.5-8 mm. long, 5-6 mm. wide; calyx-tube somewhat constricted about the middle, more or less venulose; operculum patelliform, more or less umbonate, pallid and shining, sharply circumsciss, about one-quarter the length of the bud; anthers versatile, obovate-oblong with parallel cells opening in longitudinal slits. Fruit abruptly contracted to the slender pedicels, truncate-ovoid to cup-shaped and usually slightly narrowed at the orifice, frail, striate, more or less shining, from 8 × 8 mm. up to 12 × 10 mm.; capsule deeply sunk, 3-4-locular, the valves deeply enclosed. Seeds brown, patelliform, thin, suborbicular, concavo-convex, finely reticulately pitted, scarcely marginate, 4-5 mm. long, 3-4 mm. wide, with the hilum on the concave face.

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* This difference reflects a difference in structure of the organ in the two groups. As in the majority of species, the operculum of the mature buds of the *Clavigerae* consists entirely of the inner operculum; the outer operculum is very fragile and disappears well before the bud matures. In most of the *Corymbosae,* on the other hand, the outer operculum is thickened and persistent until the bursting of the bud; there is no sharp line of abscission and the operculum tears irregularly from the calyx-tube. The inner operculum is more or less fused to the outer operculum and falls away with it.

NORTHERN TERRITORY.—Daly Range, about 12° 58′ S., 131° 8′ E., occasional at foot of stony ridge in *Eucalyptus miniata-E. tetrodonta*-dominant forest, 120 m., 13.ix.1946, *Blake* 16990; near Rum Jungle and Finniss R., about 12° 59′ S., 130° 58′ E., frequent in *E. miniata*-dominant open forest on grey, stony soil, 65 m., 8.viii.1946, *Blake* 16727; near Margaret R., 13° 2′ S., 131° 22′ E., co-dominant with *E. foelscheana* in stunted "orchard country", 17.ix.1946, *Blake* 17043; near Margaret R., about 13° 8′ S., 131° 20′ E., with *E. foelscheana* and *Xanthostemon paradoxus* on low ridge, light grey, lateritic soil, about 40 m., 27.ix.1946, *Blake* 17080; Whitestone Lagoon, 13° 2½′ S., 131° 44′ E., nearly pure stand on more or less gravelly rise, 44 m., 28.ix.1946, *Blake* 17085; about S. of Brocks Creek, between (near junction of) Hayes Creek and Douglas R., with *E. foelscheana* and *E. tectifica* in "orchard country", about 60 m., 29.vi.1946, *Blake* 16229.

Types.—Isotype of *E. clavigera*: *Cunningham* 242/1820 from Careening Bay, Western Australia (NSW, photos in BRI); leaves figured in Maiden, Crit. Rev. *Eucalyptus* 7: Plate 269, Figure 5; see also Plate 10 of this paper.

Of *E. polysciada*: barren places between Providence Hill and the Fitzmaurice River, Oct. 1855, *Mueller* (MEL, K); Plate 11.

A widely spread tree in the northern part of the Northern Territory, chiefly on shallow, stony soils, often associated with *E. foelscheana;* it extends to the Kimberley Division of Western Australia (map 4*A*).

Great confusion has arisen in connection with this species and the name applied to it. The original description was based on *Cunningham* 242/1820 from Careening Bay and it referred to a specimen carrying buds and with alternate, petiolate, oblong or ovate, glaucescent, reticulate leaves, etc. A specimen at Sydney received in 1920 from the British Museum, in flower with one bursting bud, agrees in all details with the protologue except that the twigs are quite glabrous instead of glabrous or somewhat hirsute ("glabris v. hirsutiusculis"). The sheet carries a small square paper bearing the number 242 in Cunningham's hand and a small label reading: AUSTRALIA: A. CUNNINGHAM. / 3rd VOYAGE OF "MERMAID", 1820. / Careening Bay / . (3rd, 20, and Careening Bay written in ink on the printed slip). There can be no doubt that this sheet is an isotype (Plate 10). Another isotype at Kew is represented by a photograph at Brisbane.

E. polysciada was described from specimens collected "in collibus apricis lapidosis et planitiebus aridis prope M'Adam Range."* Mueller remarked that it was allied to *E. clavigera;* he also stated that he described the bark from memory, and was somewhat doubtful about it.

The type sheet at Melbourne (Plate 11) carries several pieces (one leafy branchlet with buds and flowers, one sterile leafy twig, a leafless piece with parts of three twigs bearing many buds, flowers, and old flowers, a leafless piece with very young buds, and two detached leaves) and two packets of fragments. One of the packets contains one detached fruit in addition to buds and old flowers, and has been marked in pencil by Tovey (?) "Perhaps from New Guinea?", but the buds and their pedicels are precisely like those on the mounted pieces and differ from those of any form definitely known from New Guinea. There are three labels written up by Mueller on plain, whitish paper. One is narrower than the others and the paper is more discoloured; it reads: Arbor minor/fol. oppos. & alterna!/In plagis sterilibus/inter Providence Hill/& fl. Fitzmaurice/Oct 55. ferd Mueller/.† The other two labels are of the same width, and the bottom edge of one and the top edge of the other (which are not quite evenly cut) correspond so well that it is fairly certain that the two were written at the same time on a single piece of paper which was then divided. One of these reads: In campis steri-/lioribus ad flumen/Fitzmaurice &/ prope M'Adam/Range/Oct 55 ferd. Mueller/;‡ the other reads: Eucalyptus clavigera/A. Cunn./E. polysciada ferd Mueller/Fitzmaurice Ranges/Oct. 55. ferd Mueller/. This, and a Herbarium label reading: Eucalyptus clavi-/gera All. Cunn./Arnhem's Land/ were marked by Bentham with his familiar B on the back of the top left corner. One of two isotype sheets at Kew (photographs in BRI) carries a label in Mueller's hand reading: Eucalyptus polysciada n.sp. / Fitzmaurice / River etc. / ferd Mueller. / Both sheets were determined by Bentham as *E. clavigera.* All the plant material appears to me to belong to the same collection, and it agrees with Mueller's description. The differences in the wording describing locality and habitat on the labels and in the protologue are more apparent than real when it is realized that the Macadam Range lies between Providence Hill and the Fitzmaurice River. The smallest label appears to be the original field label. When editing Mueller's paper, Hooker referred *E. polysciada* to "E. clavigera, *A. Cunn. in hb. Hook.";* Mueller appears to have expressed his acceptance of this opinion on the other labels.

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* On sunny stony hills and arid plains near the Macadam Range.

† Smallish tree; leaves opposite and alternate!; in barren places between Providence Hill and the Fitzmaurice River. . . . .

‡ On the more barren plains at the Fitzmaurice River and near the Macadam Range. . . . .

There seems to be no doubt that *E. polysciada* and *E. clavigera* are conspecific and that Bentham was correct in treating the former name as a synonym of the latter in Fl. Aust. 3: 250 (1867). Bentham, however, extended his description to cover plants with leaves "from opposite, sessile or nearly so, and broadly ovate or almost orbicular, to alternate and broadly ovate or ovate-lanceolate . . ." and cited specimens from "Careening Bay, N.W. Coast, *A. Cunningham;* Islands of the Gulf of Carpentaria, *R. Brown;* arid rocky hills near Macadam range, *F. Mueller;* Albert river, *Henne.*" This concept has been more or less accepted by later workers.

Maiden discussed the species, op. cit. 4: 179-84 and Plate 152, Figures 1-6 (1919); his translation of the original description is extremely faulty,* but he accepted Bentham's interpretation and synonymy (he did not see the type of *E. polysciada* and copied Bentham's error in writing *polysciadia*). According to the explanation of plates on p. 199, Plate 152, Figures 1*a* and 1*b* were drawn "from a specimen collected by Allan Cunningham on the 'North-west Coast' labelled '*Eucalyptus clavigera* A.C.' by Cunningham himself, and presumably a portion of the type. Presented by Kew." Now this sheet, received mounted from Kew in 1901, carries a printed slip reading: FLORA AUSTRALIENSIS./named by Mr. BENTHAM/. The determination, *E. clavigera, A.C.*, appears on the sheet in *Bentham's* writing immediately above the slip and the appropriate reference to the Flora Australiensis (iii. p. 250) beside it. The only writing in Cunningham's hand is on a slip attached to the specimen itself and this reads merely: Eucalyptus/N.W.C./. This specimen is in young bud and has opposite, subsessile, broadly ovate-cordate, scabrous-pubescent leaves, and it certainly influenced Bentham in extending his circumscription of the species. To judge from a photograph at Brisbane, a specimen now at Kew is very like this one at Sydney, except that it has slightly longer petioles and Cunningham's label reads: N.W. Coast. / 1819 / Eucalyptus / ; it is evidently part of the same collection, gathered in the year before the type. Some of Brown's specimens cited by Bentham have similar leaves, others have quite sessile leaves. I have not seen Henne's specimens.

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* To give the correct sense of the original, the following amendations to Maiden's translation are necessary; the corresponding phrases are printed in italics: For "Branches and branchlets short, rigid, spreading, *hispid*, terete, glabrous or somewhat hirsute" read "Branches and branchlets short, rigid, spreading, *the latter* terete, glabrous or somewhat hirsute" (Ramis ramulisq. brevib. rigidis patentib., *his* teretib. glabris v. hirsutiusculis); for "pedicels elongated, striate, *on the upper side* gradually *enlarged* into *an* obconical calyx-tube" read "pedicels . . . . *in the upper part* gradually *widened* into *the* obconical calyx-tube" (pedicellis elongatis striatis, *superne* sensim in cupulam obconicam *ampliatis*); and for "operculum *finely* membraneous, *very little* depressed, scarcely umbonate" read "operculum *thinly* membranous, *quite smooth*, depressed, scarcely umbonate" (operculo *tenuiter* membranaceo *laevissimo* depresso vix umbonato).

It is now evident that Cunningham's two collections represent two quite distinct though closely allied species, and the name *E. clavigera* must be reserved for the glabrous plant with alternate, prominently petiolate, oblong or ovate leaves. It is unfortunate that this name has been commonly applied to the more or less scabrous form which is much more widely spread, and which must be called *E. confertiflora* F. Muell. Maiden, loc. cit., 181, particularly mentioned two specimens which "differ from typical *E. clavigera* in absence of hairs and in the presence of longish petioles" and figured one of them (Fig. 3), but in the explanation to plates, he stated that this figure represented a mature leaf while the figure of Cunningham's specimen was said to represent a juvenile leaf. After the sheet of *Cunningham* 242/1820 was received, Maiden (op. cit. 7: Plate 269, Figure 5) figured three leaves as "Piece of the type . . . Allan Cunningham, No. 242 . . ." but stated that they were intermediate leaves. Maiden quite overlooked the fact that this specimen differed from the other specimen which he had presumed to be the type and from the form he treated as *E. clavigera*. Blakely certainly recognized that Cunningham's two specimens represented two species, but he determined No. 242 as *E. grandifolia!*

The combination of characters that particularly distinguishes *E. clavigera* are the persistent and closely tessellated bark on the lower part of the tree with deciduous and smooth bark on the upper part, the glabrous twigs, the glabrous, prominently petiolate, oblong or ovate or oblong-lanceolate but not cordate leaves with about 18-25 pairs of lateral veins, the glabrous inflorescence with long, slender pedicels, and the thin and more or less shining operculum (27 pairs of lateral veins were counted on a few leaves of *Jensen* 354 from Rapid Creek).

Although Maiden did refer two specimens of this form to *E. clavigera*, he distributed the majority between *E. grandifolia* and *E. papuana;* the specimens with the broader leaves such as *Hill* 342, 447 were referred to *E. grandifolia* (p. 189 and Plate 154), while most of the specimens with narrow leaves, such as *Fitzgerald* 1544 and *Hill* 446 were referred to *E. papuana* on p. 195 and figured as such on Plate 155, Figures 1 and 3. This distribution of specimens accounts for some of the difficulties encountered by Maiden, Blakely, and Jacobs in distinguishing *E. papuana* and *E. grandifolia* and for their statements (at least in part) that the bark in all these species is more or less tessellated at and near the base.

In the herbarium, *E. papuana* is readily distinguished from *E. clavigera* by its short pedicels and its leaves with 28-40 pairs of lateral nerves and usually narrower, while the inflorescences are composed of fewer flowers and usually occur with the leaves. *E. clavigera, E. confertiflora,* and *E. grandifolia* resemble one another in their long pedicels and numerous flowers commonly borne on leafless branches; *E. clavigera* differs from both in the leaf venation (particularly in the better-defined intramarginal vein and the more numerous lateral veins) and more or less in leaf shape, from *E. confertiflora* also in the complete absence of indumentum and from *E. grandifolia* also in the smaller buds with smooth and shining opercula.

E. clavigera var. *diffusa* is *E. confertiflora* F. Muell. *E. clavigera* var. *gilbertensis* Maiden & Blakely resembles *E. aspera* more closely than it does *E. clavigera;* it is treated as a distinct species in this paper.

6. **Eucalyptus confertiflora** F. Muell. in J. Linn. Soc. (Bot.) 3: 96 (1859)

E. floribunda F. Muell., *loc. cit.* 83 (1859), nomen; nec Hügel (1837) nec Tausch in herb. Bauer ex Maiden (1919).

E. clavigera A. Cunn. ex Schau. var. *diffusa* Blakely & Jacobs in Blakely, Key Eucalypts 75 (1934).

Tree up to 10 m. high, with stiffly spreading, often crooked branches, stiff, brittle, and rather short twigs, and stiffly spreading, horizontal leaves; lower or greater part of trunk with persistent, grey or dark grey, roughened, closely and evenly tessellately fissured bark; remainder of tree with grey to white, smooth bark, deciduous in large, thin flakes; all younger parts scabrous-pubescent to hispid with fine, rigid, pale-coloured to ferruginous, more or less curved hairs. Juvenile leaves opposite for many pairs, sessile or nearly so, ovate to elliptic or oblong, rounded to cordate at the base, scabrous-pubescent, closely reticulate, and with as few as 6 pairs of lateral veins. Intermediate leaves much larger, up to 20 cm. long and 10 cm. wide or larger, sessile or petiolate, with more numerous lateral veins. Adult leaves opposite or alternate, sessile to distinctly petiolate with the petiole up to 1.5 cm. long, ovate or more or less elliptic or oblong or oblong-lanceolate, usually obtuse or nearly so, more or less cordate, and frequently amplexicaul, distinctly scabrous-pubescent except when very old (the hairs wearing away with age but usually persisting on the lower basal part of the midrib and the basal part of the petiole), mostly 5-15 cm. long and 2.2-10 cm. wide, 1.2-2.5 times as long as wide, prominently veined with 10-13 pairs of primary veins at an angle of usually 55°-70° (varying from 50° to 80°) with the midrib, strongly curved in the upper part and there uniting to form a very irregular and often ill-defined intramarginal vein, which is sometimes very close to the margin. Flowers very numerous, axillary, in subsessile, compound umbels or condensed corymbs, sometimes on leafless branches so that the tree appears to bear short or long, sometimes lobed or divided, dense, spiciform panicles; pedicels very slender, longer than the buds and fruits, mostly 1.5-2.5 (rarely only 1.2) cm. long, scabrous-pubescent at least towards the base, as are the other divisions of the inflorescences. Buds glabrous, pyriform, 6-7 mm. long, about 4 mm. wide; operculum patelliform, muticous or apiculate, more or less pallid and somewhat shining, from one-quarter to one-third as long as the calyx-tube. Anthers versatile, somewhat obovately oblong, with parallel cells opening in longitudinal slits. Fruits truncately ovoid or cup-shaped, very thin, venulose, from 0.8 cm. long and 0.6 cm. wide up to 1.3 cm. long and 1 cm. wide, with 3 short and broad, deeply enclosed valves. Seeds patelliform, concavo-convex, with firm margins.

NORTHERN TERRITORY.—Mary R., about 13° 5′ S., and 131° 47′ E., alluvial flat, about 60 m., 29.ix.1946, *Blake* 17090; near Brocks Creek, gentle slope with grey podsol, "orchard country" dominated by dwarf trees of *Eucalyptus foelscheana* and *E. confertiflora*, 92 m., 25.vi.1946, *Blake* 16109; about S. of Brocks Creek, between (near junction of) Hayes Creek and Douglas R., co-dominant with *E. foelscheana* in rather open tall *Eucalyptus* forest, about 55 m., 29.vi.1946, *Blake* 16236; W. of Katherine, 14° 24′ S., 131° 35′ E., mixed open forest, about 75 m., 25.x.1946, *Blake* 17300.

Types.—Of *E. confertiflora*: between the Victoria River and the Gilbert River, *Mueller;* specimen not found. Neotype: *Blake* 17300, from W. of Katherine.

Of *E. floribunda*: as for *E. confertiflora.*

Lectotype of *E. clavigera* var. *diffusa*: North Coast, *R. Brown* (NSW); figured as *E. clavigera* in Maiden, Crit. Rev. *Eucalyptus* 4: Plate 152, Figure 4.

E. confertiflora is widely spread in Northern Australia, sometimes locally co-dominant with *E. foelscheana* in "orchard country", sometimes as one of the smaller trees of the *E. miniata-E. tetrodonta* forest, and sometimes as a member of the mixed open forest of river levees and other places; it also occurs in southern New Guinea (map 1). The tree is more or less completely deciduous during part of the dry season, and the young leaves produced towards the end of this period are highly coloured with reds and purples.

This is the species that has usually been called *E. clavigera* A. Cunn. and *E. clavigera* A. Cunn. var. *diffusa* (R.Br.) Blakely & Jacobs. According to R. Kippist's footnote to the original description, Mueller used the name *E. floribunda* in his MS., apparently in ignorance of the earlier *E. floribunda* Hügel (which is usually treated as a synonym of *E. marginata* Sm.), and the name *Eucalyptus confertiflora* was substituted on pp. 96 and 100, but *E. floribunda* was allowed to remain on p. 83. The name is usually cited as *E. confertiflora* F. Muell.; I have accepted this citation because the name appeared in a paper by F. Mueller, at least three other people (J. D. Hooker, A. Black, and R. Kippist) were concerned in its publication, and it is not certain who made the substitution.

Mueller's type appears to have been lost, since no likely specimen can be found in Australian herbaria or at Kew. However, his description of the habit, bark, leaves, inflorescence, and buds accords so well with the plant described above, and excludes so completely any other species known to me from Northern Australia or elsewhere, that there can be no doubt about the application of the name. *Blake* 17300 has been chosen as neotype because it is the best material collected in the area cited by Mueller, although north of his actual route. Bentham, Maiden, and Blakely treated the name as a synonym of *E. ferruginea* Schau., probably because of the large, opposite, sessile, amplexicaul, scabrous leaves and Mueller's own remark that it was excessively close to this species. But it must be remembered that when Mueller drew up his description of *E. confertiflora,* he would have known *E. ferruginea* only from the original description, and would doubtless have been impressed by the close agreement between the foliage of his plant and that described by Schauer, particularly as Schauer's account of the inflorescence is scarcely sufficient for a critical comparison with this part of the plant. Although Mueller may have been doubtful about the correct application of Schauer's name, he had no doubts about the distinctiveness of the species, of which he gave an excellent description in his MS. as *E. undulata* (see under *E. ferruginea*).

The fruit was described in the protologue as campanulate, whereas on p. 83 (*E. floribunda*) Mueller definitely stated that the fruit was unknown and he implied (at least) that it was unknown in the key on p. 100. The description would have been drawn up in the field, but the conspectus and the key would certainly have been drawn up after his return, and I would suggest that then Mueller had only his field description of *E. confertiflora.*

E. clavigera var. *diffusa* is undoubtedly the same form. This name was published as [*E. clavigera* A. Cunn.] "Var. DIFFUSA (R.Br.MSS.), Blakely and Jacobs, var. nov." with a reference to Maiden's Critical Revision, Plate 152, Figures 4, 5, 6*a*, 6*b*. At Melbourne, there is a sheet of R. Brown's from "North Coast" with a label bearing the words *"Eucalyptus diffusa?"* in Brown's writing. This is the only earlier use of this epithet I have found. A duplicate of this collection is at Sydney, but this is now without the original label; from this Miss Flockton prepared the drawing for Figure 4 cited above, and the sheet bears her annotation "Leaves & fruits drawn 8.3.17. M.F." So far as they go, these specimens agree well enough with the description of Blakely and Jacobs; the Sydney sheet is marked TYPE and is here formally selected as lectotype because of this agreement with the description and the authors' reference to "R.Br. MSS.", even though the collection was not expressly cited in the protologue. But since Brown used the epithet as a specific epithet and wrote it with a query, and since it has never been published in this combination, it appears to be more in accord with the Rules of Nomenclature (particularly Arts. 37, 44, and 46) to cite the ternary combination as *E. clavigera* A. Cunn. ex Schau. var. *diffusa* Blakely & Jacobs.

Both *E. confertiflora* and *E. clavigera* var. *diffusa* were based on plants with sessile leaves. However, there is a form with distinct petioles, especially in the adult state when the leaves may also be alternate. It is particularly this form to which the name *E. clavigera* has been wrongly applied, but I can find no difference between them except the length of the petiole or its absence in both juvenile and adult states. Plants with long petioles are represented by *Blake* 16109, 17090 of the specimens cited above, while some of Brown's specimens at Melbourne, a specimen collected by Cunningham on the "North-west Coast" discussed under *E. clavigera* and *Specht* 227*a* are more or less intermediate.

In the adult state, all forms of *E. confertiflora* differ from *E. clavigera* in the cordate leaves with fewer and less regular veins and in the indumentum which persists at least on the base of the midrib beneath and the base of the pedicels (at least until the fruit is mature). The indefinite nature of the intramarginal vein is noteworthy. The larger adult leaves described above are found on the smaller trees and are probably comparable with intermediate leaves rather than truly adult leaves. The habit and bark are shown in Plate 4, Figure 1, and Plate 5, Figure 2.

7. **Eucalyptus grandifolia** R. Br. ex Benth. Fl. Aust. 3: 250 (1867)

Usually an erect tree up to 12 m. high, more or less completely deciduous, with a conspicuously green crown and stiff, short twigs; bark pure white, smooth and deciduous, rarely with a small amount of grey, somewhat scaly bark close to the ground. Juvenile leaves opposite, petiolate, ovate and more or less cordate, more or less hispid on the veins, petiole, and stem, prominently and irregularly veined. Intermediate leaves prominently petiolate, ovate, more or less cordate, up to about 30 cm. long and 20 cm. wide, with crinkled margins. Adult leaves opposite and alternate, petiolate, green, and more or less shining on both sides (particularly so when fresh), ovate to broadly oblong-lanceolate, acute to more or less acuminate or somewhat obtuse, broadly rounded to somewhat cordate or somewhat cuneate at the base, mostly 8.5-19 cm. long and 4.5-10 cm. wide, 1.5-3 times as long as wide, with crinkled margins; lateral veins somewhat irregular, in 13-16 pairs at an angle of 30°-60° with the midrib; intramarginal vein usually double, the outer one faint and very close to the margin, the inner one prominent and up to 4 mm. distant from the margin; petioles 1-2 cm. long. Flowers many, in compound, subsessile to shortly pedunculate, axillary, umbel-like clusters, but often on leafless branches so that the inflorescences appear to form short to very long spiciform panicles that are sometimes divided or lobed; pedicels very slender, mostly 2-3 (rarely so short as 1.5) cm. long, much longer than the buds and fruits. Buds obovoid to more or less pyriform, often more or less acuminate, 1.2-1.3 cm. long, 0.7-0.9 cm. wide; operculum greenish and dull, wrinkled, subconical, and often acuminate, one-third to one-half as long as the calyx-tube. Anthers versatile, oblong or somewhat obovate, with parallel cells opening in longitudinal slits. Fruit truncate-ovoid to cup-shaped or somewhat urceolate, thin-walled and more or less venulose, 1-1.8 cm. long and 0.8-1.4 cm. wide, with 3 short and broad, deeply included valves. Seeds irregularly or obliquely ovate to subdeltoid, patelliform, concavo-convex, with firm margins.

WESTERN AUSTRALIA.—Fifteen miles E. of Carlton Station, with *E. tectifica* in open forest on sandy soil on limestone, 29.vii.1949, *Perry* 2658. NORTHERN TERRITORY.—About S. of Brocks Creek, between (near junction of) Hayes Creek and Douglas R., "orchard country" dominated by *E. confertiflora* and *E. foelscheana*, grey podsolized soil, 66 m., 29.vi.1946, *Blake* 16228; near Ferguson R., NW. of Katherine, *Eucalyptus* forest on light grey podsol, about 145 m., 24.vi.1946, *Blake* 16089*A*; 2.9 miles S. of Daly Waters, 17.vii.1947, *Perry* 384, 385.

Duplicate types.—"Islands A and C, Carpentaria" (i.e. Sweer's Island and Allen's Isle), *R. Brown* (MEL); North Coast, *R. Brown* (NSW), figured in Maiden, Crit. Rev. *Eucalyptus* 4: Plate 153, Figures 2*a*, 2*b*.

A more or less completely deciduous tree widely spread in Northern Australia, chiefly on flat or nearly flat, ill-drained ground (map 2).

The species is distinguished from its allies chiefly by the broad, long-petiolate, shining leaves with crinkled margins, and 13-16 pairs of lateral nerves (more numerous than in *E. confertiflora*, but fewer than in the other species); by the long pedicels bearing buds larger than those of other species in the group with longer, wrinkled, and more herbaceous opercula and the frequently larger fruit. The white bark, stiff twigs, and broad, glossy green leaves give the living tree a distinctive appearance (Plate 2, Fig. 1; Plate 1, Fig. 2).

The description of the juvenile leaves given above is drawn from the reversion shoots of *Blake* 16228; they agree fairly well with the description of seedling leaves given by Maiden, op. cit. 8: 194-5.

8. **Eucalyptus aspera** F. Muell. in J. Linn. Soc. (Bot.) 3: 95 (1859)

Small tree, rarely exceeding 7.5 m. in height and often much less; bark smooth and deciduous, white or pale grey, commonly with some persistent tessellated, more or less scaly, grey bark at and near the base; branchlets hispid, densely leafy, sometimes elongated. Leaves opposite, sessile or subsessile, scabrous, oblong or ovate-oblong, more or less obtuse, cordate, mostly 2-5 cm. long and 1-2 cm. wide, mostly about 2-3.5 times as long as wide, with about 13-20 pairs of lateral veins at an angle of 60°-70° with the midrib; intramarginal vein sometimes double, the outer one close to the margin. Inflorescences axillary, of subsessile to very shortly pedunculate, 2- or few-flowered umbels; pedicels glabrous, 3-7 mm. long. Buds glabrous, pyriform, 4-5 mm. long, about 3 mm. wide; operculum patelliform, about one-quarter as long as the calyx-tube. Anthers versatile, obovate-oblong, with parallel cells opening throughout in longitudinal slits. Fruits frail, cup-shaped, 5-10 mm. long, 4-9 mm. wide; valves deeply enclosed. Seeds ovate, concavo-convex with bluntly rounded margins.

NORTHERN TERRITORY.—Hodgson Downs Station, about 15° 11′ S., 134° 4′ E., ledges of rugged barren sandstone ridges among *Plectrachne* sp., 70-75 m., 30.iv.1947, *Blake* 17539; near Three Nobs in 16° 32′ S., 135° 28′ E., dominant tree on rugged sandstone flat, 174 m., 13.v.1947, *Blake* 17747; 67 miles NE. of Cresswell Station, on outcropping quartzite near waterhole, 13.vii.1948, *Perry* 1659; Mitchiebo Waterhole, 35 miles NE. of Alexandria Station, rocky slope and crest, no soil, 24.vi.1948, *Perry* 1511.

Syntypes.—Depot Creek, March 1856, *F. Mueller* (MEL); Upper Victoria R., Dec. 1855, *F. Mueller* (MEL).

A species of distinctive appearance known from scattered localities in those parts of the Northern Territory that receive an annual rainfall of between 12 and 30 in., and the immediately adjacent parts of Queensland, chiefly from barren, stony country (map 4*B*).

E. aspera resembles *E. confertiflora* in some ways, but differs in habit, the smallness of all its parts, the more numerous lateral veins, the definite intramarginal vein, the reduced inflorescences, and the relatively short pedicels. The small but relatively broad, scabrous, cordate, more or less sessile leaves with prominent veins distinguish it from the other *Clavigerae*. The amount of rough bark is very variable.

The following specimens represent the first record of this species from Queensland:

Settlement Creek, sandstone hills, Nov. 1923, *Brass* 379; Adel's Grove (NE. of Camooweal), rocky banks, edge of cliffs and top of razor-back ridges, 18.xi.1948, *de Lestang* 417.

There are two collections in the Melbourne Herbarium that were collected by Mueller and written up by him as *Eucalyptus aspera*. The one from Depot Creek has very young buds and detached fruits, and the other from Upper Victoria River has only detached fruits. Buds were not mentioned in the original description, nor were they considered in the synopses on pp. 82 and 100, possibly because they were obviously immature. Maiden, op. cit. 4: Plate 152, Figure 1, figured specimens from the "Northern Territory" that had been received "from Melbourne Herbarium, and believed to be a portion of the type." Flowers, anthers, and fruits are figured. At least the flowers cannot be from the type and these were probably taken from *M. Holtze* 240 from Powell Creek, which is the only collection with flowers now at Melbourne. But the application of the name seems never to have been questioned and it would appear that nothing is to be gained by designating one or the other syntype as lectotype. Both specimens are meagre and unaccompanied by field notes.

9. **Eucalyptus gilbertensis** (Maiden & Blakely) S. T. Blake, comb. nov.

E. clavigera A. Cunn. ex Schau. var. *gilbertensis* Maiden & Blakely in Maiden, Crit. Rev. *Eucalyptus* 7: 432 et t. 283, fig. 8 (1928).

Species propria, ob notas sequentes praecipue distinguenda: Folia parva, breviter petiolata, opposita vel alterna, scabro-pubescentia vel tandem glabra, ovata et plus minusve cordata vel lanceolata vel linearilanceolata et utrinque acuta, eorum nervi laterales ex angulo 70°-80° a costa progredientes et in paribus 16-30 dispositi; cymae axillares pauciflorae, brevissime pedunculatae; pedicelli breves; et fructus subsessiles, fragiles, cyathiformes, 6-8 mm. longi, 6-7 mm. lati, valvis 3-4 omnino (nec profunde) inclusis. Ab *E. confertiflora* F. Muell. (*E. clavigera* A. Cunn. sensu Maiden et Blakely nec *E. clavigera* A. Cunn. ex Schau.) ob foliorum multo minorum formam atque venationem, inflorescentias paucifloras, pedicellos breves, fructus minores pro rata latiores valde diversa et *E. asperae* F. Muell. similior, a qua foliis saepe haud cordatis sed longius petiolatis tandem glabris et multo angustioribus, atque fructibus pro rata latioribus eorum valvis minus profunde inclusis, distinguenda.

A shrub or small, irregular tree up to 6 m. high; bark smooth and white or variegated with light grey, sometimes grey, persistent and scaly near the base. Branchlets subterete or slightly angular, glabrous. Leaves green or glaucescent, dull; juvenile leaves ovate, very shortly petiolate, more or less reticulate, more or less scabrous-pubescent, especially on the veins beneath; intermediate leaves up to 6 cm. long and 2 cm. wide; adult leaves opposite or alternate, shortly petiolate with the petiole up to 5 mm. long, oblong-lanceolate to narrowly lanceolate, apiculate or acuminate, rounded or attenuate at the base, finally glabrous and smooth, dull on both sides, mostly 4-6 cm. long and 0.8-1.5 cm. wide, but up to 10 cm. long and up to 2.5 cm. wide, mostly 4-6 times as long as wide; midrib slender, more or less depressed above, prominent beneath; intramarginal vein very slender, nearly confluent with the margin; lateral veins faint, in about 16-30 pairs, making an angle of 70°-80° with the midrib. Inflorescences composed of axillary, solitary, few-flowered, very shortly pedunculate cymes with very short pedicels; fruits subsessile, cup-shaped, fragile, 6-8 mm. long, 6-7 mm. wide, with 3 or 4 entirely included valves.

QUEENSLAND.—Cook District: Gilbert River, on ridges, 11.ii.1922, *White* 1392 (stunted, crooked growth; clean stem or slightly tessellated at very base); Cumberland, Gilbert R., common on desert sandstone, May 1937, *Brass* 8841 (low tree, 10-20 ft., of spreading, drooping habit; bark smooth, or sometimes rough at very base); Gregory North District: "Tranby", approx. 22° 40′ S., 142° 25′ E., on flat top of sandstone hill, about 210 m., associated with *Acacia* sp. and *Triodia* sp., 9.v.1936, *Blake* 11444 (scrubby shrub or slender, scraggy tree to 20 ft., rarely more; bark smooth, pure white or with grey patches, sometimes grey and scaly at very base; crown sparse to rather dense; leaves green or subglaucous).

Type.—*White* 1392 (NSW, BRI, MEL); figured in Maiden, loc. cit.

This species is known only from the material and notes cited above. Maiden and Blakely's original description is very brief, and Blakely's description in Key Eucalypts, 76, is not particularly satisfactory. The description given above is based on all available material.

The type collection has a large proportion of reversion shoots, and it is from these that Maiden and Blakely described the leaves. The indumentum on the specimens from the Gilbert River consists chiefly of stellate hairs, with small bristles intermixed; on the specimens from Tranby the indumentum consists almost entirely of bristle-like hairs. From its small leaves with 16-30 pairs of very oblique lateral veins, few-flowered inflorescences with short pedicels, and small fruits, *E. gilbertensis* appears to be much more closely allied to *E. aspera* than to *E. clavigera*, but differs from it chiefly in the non-cordate adult leaves on usually longer petioles and finally glabrous and smooth, and in the relatively wider fruits with the capsule less deeply enclosed; the rough bark at the base is not so thick as in *E. aspera*. It is also close to some forms of *E. papuana*, but the adult leaves have shorter petioles and fewer, more widely diverging lateral veins, and the fruits are much smaller.

Blakely, loc. cit., described the buds as "cylindroid-clavate, setose," but no buds are present on the type collection represented at Brisbane, Sydney, and Melbourne; very rudimentary inflorescences are present on Brass's specimen, and these are glabrous.

The three localities from which the species is known are shown on map 4*C*; the distribution appears to be strongly discontinuous.

10. **Eucalyptus papuana** F. Muell. Pap. Pl. **1**: 8 (1875)

E. tessellaris F. Muell. var. *dallachiana* Benth. Fl. Aust. **3**: 251 (1876).

E. clavigera A. Cunn. ex Schau. var. *dallachiana* (Benth.) Maiden in Proc. Roy. Soc. N.S.W. **47**: 77 (1913).

E. papuana F. Muell. var. *aparrerinja* Blakely in Trans. Roy. Soc. S. Aust. **60**: 154 (1936), *nomen invalidum.*

Tree, often shapely, up to 15 m. high but sometimes small, usually with a broad crown and more or less drooping branchlets; bark very white to greyish white, smooth and deciduous either throughout or else irregularly greyish- or rusty-scaly towards the base and there more or less persistent, very rarely the lower part of the trunk with an irregular development of persistent grey, flaky bark. Juvenile leaves opposite for many pairs, subsessile to shortly petiolate, oblong or elliptical to ovate-lanceolate, minutely and sparsely setose to glabrous, more or less 3-nerved at base, with as few as 5 pairs of lateral veins and the undulate intramarginal vein close to the margin, up to about 7.5 cm. long and 2.5 cm. wide. Intermediate leaves markedly different from both the earlier juvenile leaves and the adult leaves, more or less approximated in pairs, prominently petiolate, glabrous, ovate-lanceolate, and somewhat falcate, obtuse or shortly acuminate, very obtuse at the base, up to 21 cm. long and 9 cm. wide, with the intramarginal vein undulate and at some distance (up to 4 mm. or so) from the margin. Adult leaves alternate or here and there opposite, prominently petiolate, often bright green or yellowish green and shining, lanceolate or narrowly oblong-lanceolate, mostly either acute or gradually and acutely acuminate, tapering (rarely somewhat rounded) to a petiole 0.6-2.5 (mostly 0.8-2) cm. long, 5-16 cm. long, 1-4 (rarely only 0.7) cm. wide, mostly 4.5-7 but up to 8 times as long as wide, often with crinkled margins; venation very fine, the lateral veins in 28-40 pairs at an angle of 40°-60° with the midrib and the intramarginal vein distinct from the margin though mostly not more than 0.5 mm. distant from it. Flowers axillary and also terminal, in pedunculate simple umbels or small and greatly reduced corymbose panicles up to nearly twice as long as the petioles, sometimes reduced to nearly sessile clusters; pedicels 2.5-5 mm. long, shorter than the buds and fruits. Buds obovoid to somewhat pyriform, 5-6 mm. long, 3-4 mm. wide, distinct from the pedicels; operculum very short, patelliform, very thin, pallid or brownish and more or less shining. Anthers versatile, oblong-obovate, with parallel cells opening in longitudinal slits. Fruits on short pedicels with thin walls, cup-shaped to somewhat oblong-ovoid, sometimes somewhat narrowed to an indistinct neck in the upper part, abruptly rounded at the base, 1.0-1.1 cm. long, about 0.7 cm. wide, with 3 short, deeply enclosed valves. Seeds patelliform with thin margins, not winged.

NORTHERN TERRITORY.—Near (NE. of) junction of Margaret R. with Adelaide R., dominant tree on creek flat, 13.ix.1946, *Blake* 16992; near Manton Dam, 12° 53′ S., 131° 5′ E., locally dominant on lower part of gentle slope with podsolized soil, about 45 m., 18.viii.1946, *Blake* 16804; 53 miles N. of Tennant Creek, red lateritic soil, 26.iv.1948, *Perry* 614; on Rockhampton Downs Station, near the homestead, partly cleared open scrub, hard, reddish soil, 219 m., 19.v.1947, *Blake* 17859; SE. of Alexandria Station, 19° 10′ S., 136° 47′ E., stony ridge, chiefly on lower gravelly slopes, low, open, mixed scrub, 293 m., 22.v.1947, *Blake* 17919. QUEENSLAND.—Four miles S. of "Morstone", with *E. terminalis* and annuals on desert loam, 28.v.1948, *Perry* 1041.

Types.—Of *E. papuana*: *Reedy* 139 from the mainland of New Guinea opposite Yule Island (MEL); a leaf figured in Maiden, Crit. Rev. *Eucalyptus* 4: Plate 155, Figure 5.

Of *E. tessellaris* var. *dallachiana*: *Dallachy* 171, from Rockhampton (Mount Archer?; the second word on Dallachy's field label is not clear), Queensland (MEL); figured in Maiden, loc. cit., Plate 155, Figure 7*a-c*.

Of *E. papuana* var. *aparrerinja*: several syntypes, of which Basedow's specimen from MacDonnell Ranges, N. of Alice Springs, has been treated as the lectotype by Johnson in herb. Sydney.

This tree is very widely spread over the northern half of Australia and in Papua (map 3), and is found in a wide variety of habitats, from the rugged hillsides in Central Australia to the alluvial flats of the north. Several vernacular names have been applied to it, including "ghost gum" (chiefly in Central Australia), "cabbage gum", "pudding gum", "white gum", and "drooping white gum".

E. papuana has been treated as a variety of *E. tessellaris* and of *E. clavigera* (see the synonymy quoted above), but though it is closely allied to *E. tessellaris* and at times almost indistinguishable from it in the herbarium, it is so distinct in the field — even where the geographical ranges of the two forms overlap — that they must be treated as distinct species. *E. papuana* usually has a smooth, white bark throughout, sometimes becoming irregularly scaly towards the base (Plate 3, Fig. 2); only rarely does this bark persist so that a thick grey "stocking" is built up, an extreme case of which is shown by Specht's specimens from trees on

Bickerton Island and Groote Eylandt, which had rough bark 4-6 ft. from the base; however, this persistent grey bark is not so closely and neatly tessellated as it is in *E. tessellaris, E. clavigera,* and *E. confertiflora.* The pedicels resemble those of *E. tessellaris,* and are shorter than those of *E. clavigera* and *E. confertiflora.* The leaves are usually wider than those of *E. tessellaris,* usually on longer petioles and often with crinkly margins; they have fewer and fainter veins and still less prominent secondary veins and veinlets. The seeds have acute margins without the very narrow scarious border of *E. tessellaris.* The most marked difference from *E. tessellaris* is the very much wider late juvenile and intermediate leaves on longer petioles, very different from the adult leaves.

The leaves of *E. papuana* vary in colour from dull light green through yellowish green to rich green and then often more or less shining. The degree of branching of the inflorescence varies, and so does the length of the pedicels. Specimens from the more northern parts resemble the type in that the inflorescences are usually much reduced panicles of few-flowered umbels with pedicels about as long as the calyx-tube or somewhat shorter, and in the more or less flat margins of the leaves; inland specimens often have the inflorescences reduced to shortly pedunculate or even subsessile clusters of subsessile flowers, and the fruits are often wider. The extreme state with much abbreviated inflorescences and fruits wider than long corresponds to *E. papuana* var. *aparrerinja*; this is an invalid name, since it was published after January 1, 1935 without a Latin diagnosis (Art. 38, International Rules of Botanical Nomenclature).

Of the specimens cited above, *Blake* 16804 is a very good match for the specimens from New Guinea; *Perry* 614, *Perry* 1041, and *Blake* 17919 agree with the form described as *E. papuana* var. *aparrerinja*; one piece of *Blake* 16992 shows the juvenile leaves in whorls of three instead of the usual opposite arrangement.

11. **Eucalyptus tessellaris** F. Muell. in J. Linn. Soc. (Bot.) 3: 88 (1859)

E. viminalis Hook. in Mitch. J. Exped. Trop. Aust. 157 (1848); non Labill. (1806).

E. hookeri F. Muell. in J. Linn. Soc. (Bot.) 3: 90 (1859).

Tree up to 18 m. high or more with a more or less oblong or narrowly obovoid crown; lower or greater part of trunk with dark grey, closely and evenly tessellately fissured, persistent bark which changes rather abruptly to the smooth, pale grey or whitish, deciduous bark on the upper part of the tree, which is sometimes marked with darker-coloured patches before it is shed; twigs slender, pendulous. Juvenile leaves few, opposite, sessile or nearly so, narrowly ovate to narrowly oblong, more or less rounded at each end, glabrous or with scattered, minute bristles on the midrib beneath and on the stem, more or less 3-nerved at base and with as few as 5 pairs of lateral veins, up to about 5 cm. long and 2 cm. wide. Intermediate leaves few, opposite or nearly so, subsessile to shortly petiolate, lanceolate to narrowly lanceolate, relatively wider than the adult leaves (up to

11 × 1.6 cm. so far as seen). Adult leaves dull and more or less subglaucous, alternate, shortly petiolate, linear-lanceolate or linear, more or less acuminate and acute, tapering to a petiole of 0.5-1 (rarely 1.2) cm., 6.5-15 cm. long, 0.8-1.5 cm. wide, 8-15 times as long as wide, prominently and closely veined with 40-70 pairs of lateral veins at an angle of 40°-50° with the midrib and the secondary lateral and other veins equally conspicuous; intramarginal vein close to the margin. Flowers axillary (or also terminal?) in few-flowered, shortly pedunculate umbels or much reduced corymbose panicles; pedicels slender, about 2-5 mm. long, shorter than the buds and fruits. Buds pyriform, somewhat turbinate, 5-6 mm. long, 3-3.5 mm. wide; operculum patelliform, very thin, shining, about one-quarter to one-third as long as the calyx-tube. Anthers somewhat obovately oblong, versatile, with parallel cells opening in longitudinal slits. Fruits pedicellate, with very thin walls, truncately ovoid to subcylindrical, and sometimes slightly contracted above the middle, venulose, 8-12 mm. long, 6-8 mm. wide, with a more or less incurved rim and 3 short, deeply included valves. Seeds patelliform, concavo-convex, with thin, very narrowly winged margins.

QUEENSLAND.—Widely spread, chiefly on more or less distinctly sandy soils; not known from the Districts of Gregory North and Gregory South. NEW SOUTH WALES.—North-west Slopes and the northern part of the Western Plains. The distribution is shown on map 4*D*.

Types.—Of *E. tessellaris*: between Gilbert River and Carron River, *F. Mueller* (MEL); photograph in BRI.

Of *E. viminalis*: *Mitchell* 146 from "Camp XIV" (Frosty Creek, near Mt. Abundance, SE. of Roma); not seen; referred to *E. tessellaris* by Bentham and by Maiden, both of whom saw the specimen, and there are no grounds for disagreeing with their determination.

Of *E. hookeri*: as for *E. viminalis* Hook., upon which the name was based because of the earlier homonym of Labillardière.

Hybrids

Several examples of suspected hybridism have been noted between species of the *Clavigerae*. *Specht* 327*a*, 327*b*, and 327*c*, from neighbouring trees on Groote Eylandt in fruit and with photographs, suggest a small hybrid community derived from *E. papuana* and *E. grandifolia*, both of which certainly occur in the immediate neighbourhood. The trees have rough grey bark at the base like the trees of *E. papuana* on this and neighbouring islands; the fruits are like those of *E. papuana*, but with longer pedicels; the leaves are variable and some of the specimens carry reversion shoots in addition to well-developed adult leaves. The adult leaves resemble in shape those on many specimens of *E. papuana*, but they are more rigid and have fewer lateral veins; the reversion shoots recall those of *E. grandifolia* and *E. papuana* on a smaller scale, but are less hairy than those of *E. confertiflora.* According to Mr. Specht (in conversation), these reversion shoots were very numerous on some of the trees, the extreme case being represented by his 327*a*, while on others they were very few; he said that fire could not be held responsible, and certainly

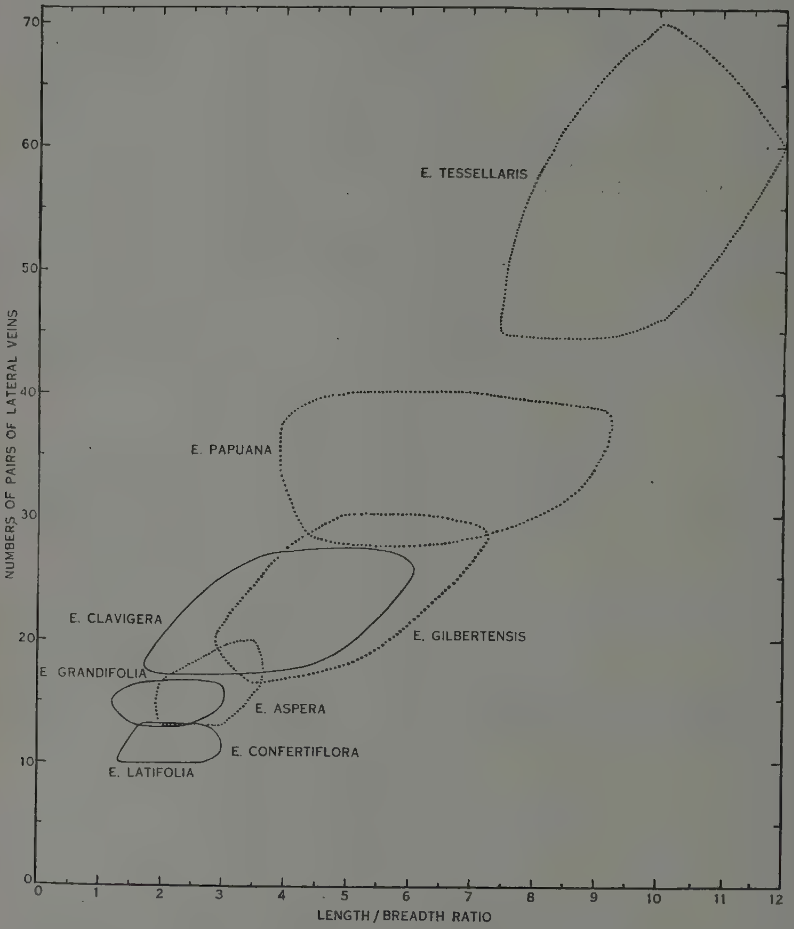

Fig. 1.—Diagram showing taxonomic relationships in the *Clavigerae;* from a scatter diagram based on the length:breadth ratio of the leaf (horizontal scale) and the number of pairs of lateral veins (vertical scale). For the sake of clarity, individual values have been omitted. Unbroken lines indicate species with pedicels as long as (usually longer than) buds and also (usually) the fruits; dotted lines indicate species with pedicels shorter than the buds and much shorter than the fruits.

the specimens give no suggestion of damage. *Specht* 634 suggests a hybrid between *E. confertiflora,* with which the tree was associated, and *E. papuana,* which was found nearby. The leaves resemble the intermediate leaves of *E. papuana,* are somewhat cordate and somewhat setose with relatively few lateral veins, approaching the general condition found in *E. confertiflora;* only a very few, old, weathered fruits were obtainable. Rather similar to these is *Jacobs* 120 from Elsey Station, consisting of material carrying minute flower-buds, which are, however, far too immature to assist in classification. Jacobs has suggested that the specimens may represent the hybrid *E. grandifolia* × *E. clavigera* (i.e. *E. confertiflora*); a relationship to *E. confertiflora* is suggested by the scabrous-pubescent younger parts and the brownish midrib, but the narrow (although more or less cordate) leaves with at least 25 pairs of lateral veins suggest *E. papuana* as a possible parent rather than *E. grandifolia.* The leaf shape and scabridity preclude the possibility that the specimens represent *E. clavigera.*

Yet another hybrid appears to be represented by *Jacobs* 107 from Maranboy Plateau, of which I have seen completely sterile material only. Jacobs has suggested that it represents *E. grandifolia* × *E. confertiflora,* a suggestion that is in accord with the more or less cordate, more or less scabrous leaves with 8-10 pairs of lateral veins.

The resemblances and differences between the species of the *Clavigerae* are partly summarized in the following key; some of them are shown graphically in Figure 1.

KEY TO THE CLAVIGERAE

Leaves distinctly cordate, more or less obtuse, 1.2-3.5 times as long as wide, usually opposite, usually sessile or nearly so, scabrous-pubescent at least on the midrib beneath and often all over; young growth more or less hispid; bark on at least the lower part of trunk grey, persistent, thickened, closely and evenly tessellated, elsewhere smooth, whitish, and deciduous:

Leaves 2-5.5 cm. long, 2-3.5 times as long as wide, with 13-20 pairs of lateral veins; pedicels 3-7 mm. long, glabrous; buds 4-5 × 3 mm.; fruits 5-10 × 4-9 mm.; tessellated bark sometimes restricted to very base .. .. *E. aspera*

Leaves usually much more than 6 cm. long, up to 15 × 10 cm. on mature twigs, up to 2.5 times as long as wide, with 10-13 pairs of lateral veins; pedicels at least 10 mm. long, mostly 15-25 mm. long, more or less scabrous-pubescent; buds 6-7 × 4 mm.; fruits 8-13 × 6-10 mm.; tessellated bark always conspicuous .. .. *E. confertiflora*

Leaves usually more or less cuneate to subtruncately rounded at the base, quite glabrous in the adult state (except sometimes in *E. gilbertensis*), alternate or opposite, always distinctly petiolate; pedicels glabrous; bark smooth or tessellated in the lower part:

Pedicels much longer than the buds and (as a rule) the fruits, 10-30 mm. long (rarely only 8 mm. in *E. clavigera*), several together in compound umbel-like inflorescences; leaves usually 1.5-4, rarely up to 6 times as long as wide; trees with rigid twigs, the flowering ones often leafless:

Buds about 12-13 × 7-9 mm.; fruits 10-18 × 8-14 mm.; leaves glossy green, undulate, 1.5-3 times as long as wide on petioles of 10-20 mm., and with 13-16 pairs of lateral veins; bark smooth almost or quite to the base .. .. *E. grandifolia*

Buds 6-8 × 5-6 mm.; fruits 8-12 × 8-10 mm.; leaves dull, 1.7-6 times as long as wide, with 18-25 (rarely up to 27) pairs of lateral veins; bark on lower part of tree grey, thickened, persistent, neatly tessellately fissured .. .. .. *E. clavigera*

Pedicels shorter than the buds and fruit, not more than 5 mm. long; adult leaves 4-15 times as long as wide; twigs usually not rigid, often very slender, the flowering ones nearly always leafy:

Adult leaves narrowed to the base, entirely glabrous and smooth; petioles 5-20 mm. long; lateral veins in 28-70 pairs at an angle of 40°-60° with the midrib; fruits 8-12 × 6-8 mm., usually pedicellate:

Bark of lower part of trunk thickened, grey persistent, closely and evenly tessellately fissured, usually sharply and rather evenly differentiated from the remainder, which is smooth and deciduous, greyish or whitish; leaves dull, more or less glaucous, with flat margins, 8-15 times as long as wide, with 40-70 pairs of lateral veins; veins and veinlets conspicuous, so that the leaf appears to be closely, finely, and evenly parallel-veined; petioles mostly 5-10 but up to 12 mm. long; juvenile and intermediate leaves usually less than twice as wide as the adult ones; seeds with narrow scarious margins .. .. *E. tessellaris*

Bark throughout smooth, white, and deciduous, or with an irregular development of scaly, more or less persistent bark close to the base; leaves often shining, sometimes bright green or yellowish green, often with conspicuously undulate margins, usually 4.5-7 (rarely up to 8) times as long as wide, with 28-40 pairs of lateral veins; only the primary lateral veins obvious, so that the leaf appears to be relatively loosely veined; petioles mostly 8-20 mm. long, rarely shorter (to 6 mm.) or longer (up to 25 mm.); juvenile and particularly the intermediate leaves up to several times wider than the adult leaves; seeds with acute, not scarious margins .. .. *E. papuana*

Adult leaves sometimes obtusely rounded at the base, sometimes scabrous with stellate hairs or setulose, sometimes very shortly petiolate, but the petioles up to 10 mm. long; lateral veins in 16-30 pairs at an angle of 70°-80° with the midrib, very obscure in old leaves; fruits more or less sessile, 6-8 × 6-7 mm. .. *E. gilbertensis*

Series Corymbosae (Benth.) Maiden

The species included here are commonly called "bloodwoods". They constitute Bentham's series *Normales,* subseries *Corymbosae* and (together with some other species) Blakely's two series *Corymbosae* (*Non-Peltatae*) and *Corymbosae-Peltatae.* The formation of Blakely's two names is contrary to Art. 26 of the International Rules of Botanical Nomenclature, and the application of at least one of them is contrary to Art. 16 and Art. 50. Although no types have been designated for the subdivisions, it seems only reasonable to accept *E. corymbosa* Sm. (*E. gummifera* (Gaertn.) Hochr.) as the type of subseries *Corymbosae* Benth. and therefore of series *Corymbosae* (Benth.) Maiden. When Blakely distinguished two series in this group, he should have used the name *Corymbosae* for the group including *E. gummifera* instead of using a new name, *Corymbosae-Peltatae;* also, he should have used the name *Corymbosae* for the subseries containing *E. gummifera* instead of his new name *Neocorymbosae.*

The *Corymbosae-Peltatae* and *Corymbosae* (*Non-Peltatae*) were distinguished solely on the presence or absence of peltate leaves among the juvenile leaves of the species; the juvenile leaves of some species are unknown, so that these had to be assigned to one or other of the groups on general resemblances. Blakely's arrangement is not followed in this paper, partly for convenience, partly because the presence or absence of peltate leaves appears to be an unreliable guide to affinities. Also, *E. clavigera* and its allies, placed in the *Corymbosae* (*Non-Peltatae*) by Blakely, appear to me to be a very distinct group, which is treated as a distinct series in this paper.

The *Corymbosae* are a very troublesome group, and this paper grew from the attempt to elucidate some of the problems encountered in studying them. The main discussion of these problems will be found under *E. terminalis, E. polycarpa, E. foelscheana,* and *E. dichromophloia.* The account given here is based on a revision of almost the whole group, which may be circumscribed as follows:

Inflorescence a terminal, corymbose panicle of umbels, sometimes leafy at the base, often very large, rarely reduced to a few flowers. Operculum not sharply circumsciss from the calyx-tube and often remaining attached to it at one side after the stamens are expanded. Flower with free part of calyx-tube more or less cup-shaped or tubular, about as wide or not much wider than the top of the ovary. Stamens all perfect; anthers versatile, obovate-oblong with parallel cells opening throughout in longitudinal slits, and with a large dorsal gland. Fruits truncately ovoid or obpyriform to ellipsoid or subglobose or more or less urceolate (with recurved rim), at least 1 cm. long (except in *E. trachyphloia* and *E. jacobsiana*), firm to woody with deeply sunk capsule and 4 or 5 deeply included valves, and with a relatively inconspicuous, in-sloping disc. Seeds large for the genus, more or less turgidly biconvex with acute edges and commonly with a long terminal wing. Cotyledons suborbicular to reniform. Juvenile leaves opposite for many pairs (sometimes one or two of the earliest "pairs" not strictly opposite), often subsessile, commonly more or less setose, sometimes peltate and then chiefly in the later stages, the earlier ones with few pairs of lateral veins. Adult leaves usually markedly different from the juvenile leaves, usually alternate and prominently petiolate, often markedly paler on the lower surface and then horizontal; lateral veins in about 30-130 pairs, nearly straight and parallel, at an angle of 50°-80° with the midrib; intramarginal vein close to the margin or more or less confluent with it (opposite, more or less sessile, and then also horizontal leaves occur in some species; those of *E. setosa*, *E. abbreviata*, and *E. ferruginea* have only 6-15 pairs of lateral veins and are not very different from the juvenile leaves). — Trees of various habit, sometimes more or less shrubby; some species are more or less deciduous during the dry season. Bark either persistent and then commonly brittle and more or less tessellately flaky or scaly (rarely long-fibrous), or else smooth and deciduous, sometimes deciduous on the upper part of the tree and persistent towards the base.

E. maculata Hook. and *E. citriodora* Hook. from eastern Australia depart somewhat from the general trend in having usually axillary corymbose panicles and sharply circumsciss opercula, the outer and inner of which are well differentiated; the fruits also are commonly three-celled.

12. **Eucalyptus setosa** Schau. in Walp. Repert. 2: 926 (1843)

E. hispida R. Br. ex Maiden, Crit. Rev. *Eucalyptus* 4: 211 (1919) *in syn.; nomen invalidum.*

A small tree with grey, flaky bark and stiffly spreading branches and branchlets; young growth more or less strongly hispid, with the bristle-like hairs extending to the buds and sometimes to the leaves. Juvenile leaves very similar to the adult leaves, but more obtuse and more definitely hispid. Adult leaves opposite, sessile or nearly so, stiffly spreading, ovate, cordate, acute to somewhat obtuse, cuspidate, 1.7-2.2 times as long as wide, usually 5-10 cm. long and 3-5 cm. wide, smooth or scabrous to more or less hispid, particularly at the margins; lateral veins in 9-12 pairs at an angle of 55°-75° (rarely 50°) with the midrib, curved towards the margin. Inflorescence about as long as or a little longer than the leaves; pedicels 0.5-2 cm. long. Buds more or less setose, more or less pyriform, with a poorly differentiated operculum ending in a subentire or variously toothed point or tail, about 1.3 cm. long and 1 cm. wide. Anthers obovoid-oblong, versatile, with parallel cells opening in longitudinal slits. Fruits woody, subglobose to somewhat obpyriform, 1.5-3 cm. in diameter, commonly more or less setose, with a narrow rim and deeply enclosed valves. Seeds with a long terminal wing.

NORTHERN TERRITORY.—Between Magela Creek and East Alligator R., about 12° 36′ S. and 132° 52′ E., base of hill, mixed open forest, 2.x.1946, *Blake* 17146; E. of

Mary R., 13° 5′ S., 131° 50′-55′ E., occasional in open *Eucalyptus* forest, more or less stony ground, about 70 m., 29.ix.1946, *Blake* 17094; Daly R., about 13° 45′ S., and 130° 42′ E., rocky hill in open forest, about 30 m., 25.vii.1946, *Blake* 16628; about SSE. of mouth of Daly R., 13° 51′-53′ S., 130° 20′-30′ E., low, rocky hill, open *Eucalyptus* forest, about 85 m., 25.vii.1946, *Blake* 16615; S. of Elliott, 7.vii.1947, *Perry* 239; 6.5 miles S. of Elliott, 9.vii.1947, *Perry* 293; near (E. of) Lake Woods, in *Acacia-Triodia* scrub, 2.xi.1946, *Blake* 17357; 50 miles N. of Tennant Creek, deep red, sandy soil, 26.iv.1948, *Perry* 613. QUEENSLAND.—Fifty-six miles N. of Lawn Hill Station, flat top of laterite hill, 1.vi.1948, *Perry* 1138.

Type.—Islands of the Gulf of Carpentaria, *Brown and Bauer* (W, BRI); figured in Maiden, Crit. Rev. *Eucalyptus* 4: Plate 157, Figure 5.

Rather widely spread in the more northern parts of the Northern Territory, in the adjacent parts of Western Australia, and in north-western and central Queensland, chiefly on rocky or sandy ground (map 13).

I have seen abundant fruiting material of this species, but very little in bud and flower. The length of the pedicel is very variable. The small, broad, cordate, opposite, sessile or subsessile leaves with few pairs of lateral veins and the hispid twigs and young growth make the species an easy one to recognize; habit and bark are shown in Plate 6, Figures 1 and 2.

Maiden's figure of the type is exactly matched by a specimen at Brisbane with a rough label in Brown's writing, which reads: . . . Island C/landed 20 Nov 1802 . . . On this date, as shown in Flinders' Voyages 2: 136 (1814),* Brown and Bauer collected together on Allen's Isle, one of the Wellesley Islands, Gulf of Carpentaria. The specimens collected by Brown and Bauer are in bud. Specimens at Brisbane from the nearby Sweer's Island and from Normanton agree closely as to foliage, but are in fruit, and these are more or less closely matched by the remainder of the Queensland material; the leaves are nearly glabrous and the fruits are about 1.6-2 cm. in diameter. The specimens from the Northern Territory, particularly from the northern parts, mostly have larger leaves, which are often more or less strongly setose, and much larger fruits up to 3 cm. in diameter. *Blake* 16628 is noteworthy in that some of the pieces have almost quite glabrous twigs and pedicels, which are also more or less pruinose, while the buds are glabrous except for rudimentary bristles on the operculum; other pieces are quite like the majority of the specimens and parts are very like Brown's specimen; the fruits are large, 2.8-3 cm. in diameter. The material forming this collection came from a few trees on the top of a small hill; there seems no doubt that only one species is represented.

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* "Saturday 20. In the morning we steered toward Allen's Isle . . . our latitude here was 17°5′, longitude 139°26′; . . . I went on shore with the botanical gentlemen . ."

13. **Eucalyptus ferruginea** Schau. in Walp. Repert. 2: 926 (1843)

E. undulata F. Muell. ex A. Black in J. Linn. Soc. (Bot.) 3: 95 (1859), *in syn. in nota, nomen invalidum;* non G. Don (1830), *nomen nudum;* nec Oldfield ex Maiden (1902), *in syn.;* nec Tausch ex Maiden (1907), *in syn.*

Usually a widely spreading tree up to about 12 m. high; bark persistent throughout, grey, shortly fibrous, and flaky. Twigs, foliage, and inflorescence covered with a close, dense, ferruginous indumentum of small, more or less stellate scales mixed with short bristles, which are often more or less branched or barbellate, the indumentum tending to wear away with age and then often becoming somewhat silvery. Juvenile leaves very similar to the adult leaves, except that they are shorter and blunter. Adult leaves opposite, subsessile (petioles up to 5 mm. long), stiffly spreading, elliptical or oblong-ovate (1.6-3 times as long as wide), obtuse and cuspidate to acute or abruptly acuminate at the apex, narrowly cordate at the base, often undulate, mostly 8-13 cm. long and 3-7 cm. wide, ferruginous to somewhat silvery or nearly green; lateral veins in 6-10 pairs, at an angle of 50°-60° (sometimes 65°) with the midrib, curved towards the margin. Inflorescence much longer than the leaves with more prominent bracts than are usual in the genus; pedicels very short or up to 4 mm. long, stout. Buds stellate-scaly, more or less pyriform, about 1.2 cm. long and 1 cm. wide. Fruits truncately ovoid or ellipsoid, 2-2.5 cm. long, 1.5-1.8 cm. wide, more or less scaly, with a rather thin rim and deeply enclosed valves. Seeds with a long terminal wing.

NORTHERN TERRITORY.—E. of Mary R., 13° 5′ S., 131° 50′-55′ E., occasional in open *Eucalyptus* forest, flat, more or less stony ground, about 70 m., 29.ix.1946, *Blake* 17093; about SW. of Katherine, 14° 34′ S., 132° 4½′ E., mixed open forest, gentle slope, reddish sand, 107 m., 11.x.1946, *Blake* 17202; 4.1 miles E. of "Dunmarra", 15.vii.1947, *Perry* 381.

Types.—Of *E. ferruginea*: Gulf of Carpentaria, *Brown and Bauer* (W, NSW, MEL, BRI); figured in Maiden, Crit. Rev. *Eucalyptus* 4: Plate 159, Figures 1-3.

Of *E. undulata*: not found.

Known only from the northern part of the Northern Territory and the extreme north-west corner of Queensland.* It is usually scattered through the mixed open forest, chiefly on sandy or stony soils (map 14*A*).

E. ferruginea resembles *E. setosa* in many respects, but it is a larger tree with larger leaves and narrower fruits; it is well distinguished by the characteristic stellate-scaly indumentum of the leaves and buds and a coarser indumentum on the twigs, but this indumentum wears away with age. Some old leaves on *Blake* 17093 and on Jensen's specimens from the Nicholson R. are glabrescent and glaucous, with relatively few of the characteristic scales left; *Perry* 381 has green, almost glabrous leaves, but they are much damaged. *Jacobs* 139 has narrower leaves (about 2.7-3.5

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* Between Turn-Off Lagoon and Woologorang, May 1940, *Jensen* 45; Nicholson R., May 1940, *Jensen*. This is the first definite record of this species from Queensland.

times as long as wide), longer petioles (up to 7 mm.) and smaller fruits (1.5 × 1.2 cm. up to 2 × 1.4 cm.) than on other specimens seen. One shoot with juvenile leaves in *Blake* 17202 has ternate leaves; the other shoots have the usual opposite leaves.

14. **Eucalyptus abbreviata** Blakely & Jacobs in Blakely, Key Eucalypts 77 (1934)

Small tree up to 6 m. high; branches spreading and descending. Bark persistent, grey (?), rough, and flaky-looking, deeply furrowed longitudinally and less so horizontally. Twigs pale grey, terete, glabrous. Juvenile leaves not seen. Adult leaves opposite or nearly so, sessile or nearly so (petioles up to 2.5 mm. long), rigid, somewhat yellowish green, paler beneath, narrowly ovate to lanceolate or oblong-lanceolate, 1.8-3.6 times as long as wide, more or less acute or shortly acuminate, cordate and more or less amplexicaul, sparsely hispidulous or glabrescent, flat or undulate, 7-16.5 cm. long, 3-7.6 cm. wide; lateral veins in 12-15 pairs, at an angle of 50°-65° with the midrib, mostly curved towards the margin; intramarginal vein slightly irregular, close to or somewhat distant from the edge. Inflorescence contracted and very short; pedicels short and thick, up to 6 mm. long. Buds obovoid, gradually narrowed to the pedicels, slightly scurfy, about 1.2 cm. long and 1 cm. wide; operculum more or less patelliform, about one-quarter as long as the calyx-tube. Anthers versatile, nearly oblong, with parallel cells opening in longitudinal slits. Fruits obpyriform to somewhat urceolate, thick and woody, abruptly contracted to the pedicel and with a short, nearly cylindrical neck, nearly smooth, pale-coloured, 3-3.5 cm. long, 2.3-2.7 cm. wide; rim thick, obtuse; valves 4 or 5, very deeply enclosed. Seeds with a long terminal wing.

NORTHERN TERRITORY.—Twelve miles from "Willeroo" on road to Katherine, forming parkland with *E. pruinosa*, *Themeda australis*, and *Heteropogon contortus*, 3.vi.1949, *Perry* 2018.

Type.—Jacobs 105, from between Katherine and Maranboy (NSW, AFSC, BRI); Plate 12.

Known only from the two collections cited above (map 7*D*). It is closely allied to *E. ferruginea*, from which it differs in the almost complete absence of indumentum, a tendency to pruinosity, the slightly more numerous lateral veins, the very short inflorescence, and the much larger, coarser, glabrous, obpyriform or urceolate fruits. The fruits resemble those of *E. zygophylla* more than those of any other species, but the leaves have fewer lateral veins, and are never connate.

15. **Eucalyptus terminalis** F. Muell. in J. Linn. Soc. (Bot.) 3: 89 (1859); non Sieb. ex Benth. Fl. Aust. 3: 211 (1867) *in syn., nomen invalidum*

E. pyrophora Benth. Fl. Aust. 3: 257 (1867).

E. macropoda Blakely, Key Eucalypts 87 (1934); *syn. nov.*

A tree usually not exceeding 10 m. in height and sometimes small and somewhat shrubby; bark variable, usually smooth, white, and deciduous on the upper part, and persistent, scaly, and mottled rusty and pale grey towards the base, less commonly becoming thicker and flaky on the trunk. Juvenile leaves not peltate. Intermediate leaves mostly broader, blunter, and on shorter petioles than the adult ones. Adult leaves alternate, petiolate, thick, about the same colour on both sides, dull and pallid or yellowish, lanceolate, acute or acutely acuminate to somewhat obtuse, narrowed to a petiole of 1.5-2.5 cm., 3.5-9 (rarely up to 11) times as long as broad, faintly nerved with a large number (more than 40 pairs) of lateral veins at an angle of 50°-60° with the midrib, and the intramarginal vein very close to the thickened margin. Inflorescence a large, terminal, corymbose panicle, rarely reduced to a few flowers, the branches sometimes thick and swollen; pedicels variable, 0.5-1.7 cm. long, sometimes relatively slender. Buds turbinate-obovoid, gradually narrowed to the pedicels, pallid to nearly white, more or less scurfy, from 9 mm. long and 6 mm. wide up to 14 mm. long and 9 mm. wide; operculum from one-quarter to nearly one-half as long as the calyx-tube and nearly as wide as it, shallowly rounded or apiculate. Anthers obovate-oblong, versatile, with parallel cells opening in longitudinal slits. Fruits thick and woody, dull and pale-coloured, from obpyriform to ovoid or oblong-ovoid, widest distinctly below the middle and with only an indistinct neck, 1.7-4 (usually at least 2) cm. long and 1.3-2.3 cm. wide, with a thick, often obtuse but not spreading rim and deeply included valves. Seeds with a long terminal wing.

NORTHERN TERRITORY.—Katherine, gentle slope towards river, mixed open *Eucalyptus* forest, 107 m., 9.x.1946, *Blake* 17187, 17188; 25 miles SSE. of Victoria River Downs Station, desert loam with annuals, 12.vi. 1949, *Perry* 2143. QUEENSLAND.—Three miles from Doomadgee Mission, on levee, 1.vi.1948, *Perry* 1148.

Types.—Holotype of *E. terminalis*: Arnhem Land, *F. Mueller* (MEL); Plate 13, Figure 1.

Lectotype of *E. pyrophora*: Upper Victoria R., *F. Mueller* (MEL); figured in Maiden, Crit. Rev. *Eucalyptus* 4: Plate 166, Figure 1; and Plate 13, Figure 2 of this paper.

Holotype of *E. macropoda*: *Fitzgerald* 1012 from Packhorse Range, Western Australia (NSW); figured in Maiden, op. cit. 6: Plate 236, Figure 2, under *E. collina* W. V. Fitzg.

A tree of somewhat varied habit, widely spread in Australia, extending to the more arid regions within the 10-in. isohyet in Central Australia, south-western Queensland, and north-western New South Wales, and to the north in the region of the 40-in. isohyet. Usually it is found on ground with fairly good water relationships (map 5*A*).

This species has usually been known as *E. pyrophora*. The name *E. terminalis* has been misapplied to *E. polycarpa* since the days of the Flora Australiensis, but it has also been used for other allied species. In Illustr. Bot. Captain Cook's Voy. 2: 39 and Plate 117 (1901), Britten applied the name to specimens of the very different *E. crebra* F. Muell.

E. terminalis Sieb. has never been validly published; according to Bentham, and Maiden (Crit. Rev. *Eucalyptus* 2: 107 (1911)), the name appeared on a label accompanying a specimen of *E. paniculata* Sm. *E. terminalis* var. *longipedata* Maiden & Blakely is *E. bleeseri* Blakely.

Jacobs (op. cit., pp. 17-19) discussed what he appropriately termed "The Bloodwood Puzzle." He pointed out that the leaves of the species commonly called *E. terminalis* are markedly paler on the under side, although in the original description of the species they were said to be of the same colour on each side; also that *E. polycarpa* was originally described as having leaves "a little paler on the under side."

Further difficulties arose when the N.A.R.S. collections were studied. It became clear that Maiden had accepted as the type of *E. polycarpa* a specimen that had been collected 13 years after the species was described; that he had so poorly translated Mueller's original descriptions of *E. polycarpa* and *E. terminalis* that his versions give a quite different impression of these species than do Mueller's originals;* and that he did not see Mueller's specimens of either *E. polycarpa* or *E. terminalis* and entirely misunderstood both species.

Both *E. polycarpa* and *E. terminalis* were described from fruiting specimens. As shown by his determinations in the Melbourne Herbarium, Mueller gradually extended the use of the name *E. terminalis* to cover a wide variety of forms, sometimes including *E. polycarpa.* Perhaps influenced by Mueller's determinations on the specimens Bentham (Fl. Aust. 3: 257) treated *E. polycarpa* as a synonym of *E. terminalis* and then described *E. pyrophora* principally from three collections, two of them in bud and flower and one in fruit. The specimens in fruit appear to belong to *E. dichromophloia,* and in 1919 Maiden (loc. cit. pp. 320-1) typified *E. pyrophora* on Mueller's two collections in bud and flower from the Upper Victoria River and Depot Creek; both specimens at Melbourne had been labelled *Eucalyptus terminalis* by Mueller before they were seen by Bentham, but they were evidently not considered when the original description of *E. terminalis* was drawn up.

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* Maiden's translation in Crit. Rev. *Eucalyptus* 4: 321 (1919) of Mueller's account of *E. polycarpa* is especially inaccurate. Among the more serious errors may be mentioned:

1. The rendering "The terminal umbels in a broad panicle of 4-6 flowers" for "umbellis terminalibus ample paniculatis 4-6-floris"; a better translation would be "umbels 4-6-flowered in large terminal panicles".

2. The translation of the word "passim" in the notes on distribution as "everywhere" instead of "here and there" or "scattered".

3. The rendering ". . . with the bark persistent, the outside falling off in dirty grey rough and wrinkled flakes. The inside brownish and coming away in little pieces . . ." for ". . . cortice ubique persistente, extus sordide cano rugoso et rimoso, intus fuscescente, in frustulis separabili . . ." A better translation would be ". . . with the bark persistent throughout, dirty (light) grey, wrinkled, and cracked on the outside, becoming fuscous within, separable (i.e., capable of being separated) in small pieces . ."

In *E. terminalis* (loc. cit. 305), the errors are not so serious, but the translation of the description of the bark gives a quite wrong impression. Instead of Maiden's "The bark dark fuscous, persistent, wrinkled and scaly, brown or ferrugineous within, coming away somewhat tardily in irregular flakes" for Mueller's ". . . cortice sordide fusco persistente rugoso rimosoque intus fulvo vel ferrugineo in frustulis irregularibus vix parce secedente", it would be better to read ". . . bark dirty fuscous, persistent, wrinkled and cracky, tawny or rusty within, coming away rather freely (literally: scarcely sparingly) in irregular small pieces."

The type of *E. terminalis* evidently became mislaid. Apparently, it was not seen by Bentham, for his description of this species refers entirely to *E. polycarpa;* in particular, his description of the fruits cannot refer to the fruits of *E. terminalis* as described by Mueller. In the Melbourne Herbarium, in a folder with specimens of *E. intermedia* R. T. Baker from the Hastings River, New South Wales, I found a collection of four loose leaves and four fruits in varying stages of maturity, enclosed in a packet similar to those used by Mueller on the Gregory Expedition and which was marked by Mueller "Euc. terminalis!! Arnhems Land". This is the only fruiting specimen yet located that was collected by Mueller on the Gregory Expedition and also marked by him with this name. So far as it goes, it agrees with the original description and there seems no doubt that it is the type of the species. The leaves agree with those on the lectotypes of *E. pyrophora.* Further, *Blake* 10102 (from Cloncurry, Queensland) carries buds, flowers, and mature fruits; except for their maturity, the fruits are a good match for those of the type of *E. terminalis,* while the flowering twigs are an excellent match for the lectotypes of *E. pyrophora* (Plate 13). Mueller's description of the bark etc. of *E. terminalis* also applies to the tree from which my specimens were taken. There can be no doubt that *E. pyrophora* is conspecific with *E. terminalis,* and it may be noted that Mueller commonly regarded these two names as synonymous, as in Fragm. **11:** 42 (1878) and Eucalyptogr. dec. 5, under *E. corymbosa* (1880). (A photograph of a better sheet of Mueller's collection at Kew was received after the paper left my hands. Bentham annotated the sheet, but the immaturity of the fruits must have led him to ignore the specimen when preparing his description.)

The type of *E. polycarpa* is more satisfactory, and one of the labels bears the description of the bark given in the original description (Plate 14). It represents the species that has commonly been called *E. terminalis* and the original description and notes agree with this species. For some unexplained reason, Maiden (Crit. Rev. *Eucalyptus* 4: 321-2 (1919)), treated as the type of *E. polycarpa* a specimen collected by Giles in Central Australia 13 years after the species was described. I believe this specimen represents a form of *E. terminalis* as interpreted here. Maiden at first treated his concept of *E. polycarpa* as a variety of *E. pyrophora,* but later (Crit. Rev. *Eucalyptus* 8: 71 (1929)) he treated it as a distinct species on the grounds that it had smaller and thinner fruits and slender panicle branches, which were not swollen as they were said to be in *E. pyrophora.*

Blakely (Key Eucalypts, 17 and 87) also stressed the swollen panicle branches of *E. pyrophora,* but both Maiden and Blakely have completely ignored the fact that the panicle branches on the lectotype of *E. pyrophora* (as selected and figured by Maiden himself) are not swollen; swollen branches like those figured by Maiden (Crit. Rev. *Eucalyptus* 4: Plate 166, Fig. 2*b*) occur in other species and appear to be pathogenic in nature.

E. macropoda was founded on a single small specimen in flower and bud with a loose, much-weathered fruit; the noteworthy features are the long and rather stout pedicels, the coarse buds and flowers, and the long, nearly cylindrical fruit. The fruit (so far as its condition permits comparison) and leaves are matched by *Jacobs* 117 from Mataranka; my specimens from Katherine are not very different except for the shorter pedicel. The buds, flowers, and pedicels are coarser than any I have seen on other specimens of *E. terminalis,* but are otherwise similar.

A photograph of a tree of *E. terminalis* near the type locality of *E. pyrophora* is reproduced as Plate 7.

The species is best distinguished from its allies by the following combination of characters: narrow, thick, dull leaves about the same colour on both surfaces; relatively large, pallid, and scurfy-looking to nearly white buds that taper gradually to their pedicels; and the large, coarse, woody, pale-coloured but dull fruits usually at least 2 cm. long, which are widest distinctly below the middle with an indistinct neck in the upper part and with a thick, often obtuse, but not spreading rim. As a rule, there is some scaly, mottled rusty and pale grey bark towards the base of the tree passing into smooth, whitish, deciduous bark on the upper part, with the proportion of scaly and persistent bark to the smooth and deciduous bark varying in the same way as it does in *E. latifolia, E. dichromophloia,* and *E. foelscheana.* The specimens from Katherine are from trees with thicker, more persistent bark than is usual for the species; the locality is the most northerly yet known. Some fruiting specimens from Central Australia have fruits only 1.5 cm. long and very narrow leaves; they show a distinct approach to *E. dichromophloia,* but in the absence of buds they are referred to *E. terminalis* because of the thick, woody walls of the fruit and its thick, scarcely spreading rim. *E. foelscheana* may be distinguished by its broad leaves and the usually thinner and often spreading rims to the often reddish and somewhat shining fruit; also the buds are less scurfy and often reddish, and the intermediate leaves are very much larger.

16. **Eucalyptus polycarpa** F. Muell. in J. Linn. Soc. (Bot.) 3: 88 (1859)

E. terminalis F. Muell. var. *carnosa* F. M. Bail. in Qd. Agric. J. 15: 898 (1905), *nomen provisorium et seminudum.*

E. pyrophora Benth. var. *polycarpa* (F. Muell.) Maiden, Crit. Rev. *Eucalyptus* 4: 321 (1919), *quoad basonym.*

A tree, often shapely, up to about 15 m. high, with grey, more or less tessellately fissured and flaky and rather soft bark extending to the small branches and brown on fracture. Juvenile leaves not peltate, shortly petiolate, hispid or setose. Intermediate leaves not very different from the adult leaves except that they are shortly petiolate, sub-opposite, and less acute. Adult leaves alternate, petiolate, markedly paler on the lower surface, narrowly lanceolate, about 5-8 times as long as wide, about 10-18 cm. long and 1.3-2.8 cm. wide, with 40 or more pairs of lateral veins at an angle of 60°-70° with the midrib; intramarginal vein contiguous to or more or less confluent with the thickened and somewhat recurved margin on the upper surface, distinct from it on the lower surface. Flowers in large, terminal, corymbose panicles; pedicels relatively short, but varying from 3 to 12 mm. long. Buds pyriform, prominently scurfy, with a very short operculum not sharply distinguished from the calyx-tube, in all 10-13 mm. long and 6-9 mm. wide. Anthers obovate-oblong, versatile, with a dorsal gland and parallel cells opening in longitudinal slits. Fruits on slender pedicels shorter than the width of the fruit, more or less scurfy, 1.5-3 cm. long, 1-1.5 cm. wide, 1.5-2.5 times as long as broad and broadest at or about the middle, more or less elliptic to oblong in outline, sometimes with a distinct neck; rim rather thin, erect or slightly excurved; valves deeply included, usually 4. Seeds with a long terminal wing.

NORTHERN TERRITORY. Near Margaret R., in about 13° 6′ S. and 131° 22′ E., river flat, hard, grey soil, about 30 m., 21.ix.1946 *Blake* 17076; between (near junction of) Daly R. and Douglas R., in open, mixed, *Eucalyptus*-dominant forest, grey, gravelly soil, about 52 m., 30.vi.1946, *Blake* 16245; 7 miles N. of Leguna Station, dominant tree in open forest on deep sandy soil, 27.vii.1949, *Perry* 2594; about 20 miles SW. of Leguna Station, alluvial deep sandy yellow podsol, 28.vii.1949, *Perry* 2631; 61.5 miles from "Beetaloo" on the road to "O.T.", 11.vii.1947, *Perry* 319. QUEENSLAND. Thirty-seven miles N. of Lawn Hill Station, open forest with *E. microtheca*, 31.v.1948, *Perry* 1113.

Types.—Of *E. polycarpa*: "Arnhem Land, 25 July 1856", *F. Mueller* (MEL); at this date, Mueller was near the Cox R., N. from the site of the present "Tanumbirini" homestead; sheet figured in Plate 14.

Of *E. terminalis* var. *carnosa*: two syntypes — Gowrie, *F. M. Bailey* (BRI), and 74 miles, Central Railway, received from Chief Engineer of Railways (BRI).

This species is very widely spread over the northern half of the continent and in southern New Guinea (map 8). In the Northern Territory, it generally occurs on alluvial flats and along the edge of broad, shallow drainage channels, usually as scattered trees; it has also been observed in open communities associated with *Melaleuca* sp. on deep, sandy soils, and in other habitats.

E. polycarpa is distinguished from its allies chiefly by the following combination of characters: rough, tessellated bark throughout, which is brown on fracture; narrowly lanceolate, markedly discolorous leaves;

mostly relatively short pedicels; prominently scurfy buds with a very short operculum not sharply marked off from the calyx-tube; the medium-sized but narrow fruits at least 1.5 times as long as wide, broadest at or very shortly below the middle; seeds with a long terminal wing; and the juvenile leaves not peltate.

Of the specimens cited above, *Blake* 16245 resembles the type very closely with the fruits about 1.7 cm. long and 1 cm. wide; *Blake* 17076 has very much longer fruits, up to 3 cm. long and 1.3 cm. wide, usually with a prominent neck. Most of the numerous specimens examined have fruits intermediate in size and shape.

As shown in the discussion under *E. terminalis*, the name *E. terminalis* has commonly been applied to this species and the name *E. polycarpa* has been applied to forms of *E. terminalis* and *E. dichromophloia; E. polycarpa* var. *oligocarpa* is a form of *E. dichromophloia. E. terminalis* var. *carnosa* was mentioned more or less incidentally by Bailey without any description other than the remark that "the fruits are of a more fleshy nature than any of the gums with which I am acquainted." The specimens carry immature fruit.

The name *E. pyrophora* var. *polycarpa* was based nomenclaturally upon *E. polycarpa* F. Muell., but the specimens referred to it by Maiden are of *E. terminalis.*

Two species allied to *E. polycarpa* from eastern Australia are discussed under *E. gummifera* and *E. intermedia.*

17. **Eucalyptus bleeseri** Blakely in J. Roy. Soc. N.S.W. **61**: 175 (1927)

E. terminalis F. Muell. var. *longipedata* Maiden & Blakely in Maiden, Crit. Rev. *Eucalyptus* 7: 407 (1928).

Tree to about 15 m. high with smooth, white, deciduous bark with usually some rusty, subpersistent, scaly bark towards the base. Juvenile leaves suborbicular to broadly ovate or elliptic, rounded to cordate at the base and a few upper ones peltate, shortly petiolate, scabrous-setose. Adult leaves lanceolate, acutely acuminate, more or less falcate, narrowed to the petiole of 1-2 cm., mostly 7.5-12.5 cm. long and 1-2.2 cm. wide, 4-9 (mostly 5-7) times as long as wide, shining green above, paler and duller beneath, the venation very faint with the intramarginal vein contiguous to the margin and 45-60 or more pairs of lateral veins at an angle of about 50°-60° with the midrib. Flowers in terminal corymbose panicles shorter or longer than the leaves; pedicels slender, 1-2 cm. long. Buds oblong or oblong-obovoid, neither scurfy nor scaly, abruptly contracted to the pedicels, about 1.2-1.3 cm. long and 0.7 cm. wide; operculum more or less hemispherical, finely wrinkled, about one-third as long as the calyx-tube. Anthers oblong-obovate, versatile, with parallel cells opening in longitudinal slits. Fruits on slender pedicels as long as the width of the fruit or longer (1.2-2 cm. long), truncately oblong-ovoid, widest a little below the middle, with an indistinct neck and a rather acute rim, 1.6-2.2

cm. long, 1.1-1.4 cm. wide, about 1.5 times as long as wide, with 3 or 4 deeply enclosed valves.

NORTHERN TERRITORY.—Near (about NW. of) Brocks Creek, in *Eucalyptus* forest, grey rather shallow loam, 70 m., 7.vii.1946, *Blake* 16380.

Types.—Of *E. bleeseri*: Darwin, *Bleeser* (NSW).

Of *E. terminalis* var. *longipedata*: *Allen* 181 from Darwin (NSW); figured in Maiden loc. cit., Plate 280, Figure 4.

A rather conspicuous tree of the taller *Eucalyptus* forest of the northern part of the Northern Territory (map 12), readily recognized in the field by the shining green narrow leaves, and smooth, white bark, more or less rusty-scaly towards the base, and in the herbarium by the narrow, discolorous leaves associated with long pedicels, smooth buds, and smooth, relatively narrow fruits. Its habit is shown in Plate 6, Figure 4.

Herbarium material closely resembles that of *E. polycarpa*, but the buds are more oblong and smooth (except for the finely wrinkled operculum), the fruits are smooth or nearly so, and the pedicels are much longer.

18. **Eucalyptus dichromophloia** F. Muell. in J. Linn. Soc. (Bot.) 3: 89 (1859)

E. niphophloia Blakely & Jacobs in Blakely, Key Eucalypts 79 (1934).

E. erythrophloia Blakely, Key Eucalypts 80 (1934).

E. arenaria Blakely, Key Eucalypts 81 (1934).

E. polycarpa F. Muell. var. *oligocarpa* Blakely & Jacobs in Blakely, Key Eucalypts 86 (1934).

Tree, sometimes small and shrubby, sometimes up to 12 m. high with usually a short trunk; twigs slender, angular; bark for the greater part smooth, white, and deciduous, towards the base with some persistent, scaly, and rusty or reddish and pale grey mottled bark, which is sometimes almost absent but sometimes extends over the greater part of the tree. Cotyledons slightly reniform. Juvenile leaves opposite for several pairs, shortly petiolate, elliptic or ovate, and more or less obtuse to oblong-lanceolate and acute, rounded to slightly cordate at the base but not peltate, more or less setose or scabrous on both sides, the paler lower surface also closely but minutely white-pubescent, the intramarginal vein somewhat distant from the slightly recurved margin, loosely and faintly reticulate with as few as 10 pairs of lateral veins. Intermediate leaves becoming glabrous and lanceolate to broadly lanceolate, up to about 20 cm. long and 10 cm. wide. Adult leaves alternate, usually slightly paler beneath, lanceolate (usually narrowly so), acute or acuminate, tapering to a petiole mostly 1-2 cm. long but varying from 0.9 to 2.5 cm., 8-20 cm. long, 1-4.2 cm. wide, usually more than 3 and up to 14 times as long as wide, the wider ones (if present) associated with narrow ones, thick and faintly nerved with 30-80 pairs of lateral veins at an angle of 60°-70° with the midrib and the intramarginal vein almost confluent with the margin in the narrower leaves but undulate and up to 1.5 mm. or more distant in the wide ones. Inflorescence a terminal, corymbose panicle, sometimes large and more or less exceeding the leaves, sometimes reduced to a few flowers; pedicels slender, 2-5 mm. long. Buds rounded-obovoid, abruptly contracted to their pedicels, usually smooth and reddish but often whitish and somewhat scurfy, 5-7 mm. long and 3-6 mm. wide; operculum about one-third as long as the calyx-tube and slightly narrower than it, flatly rounded to somewhat conical. Anthers versatile, obovate-oblong, with parallel cells opening in longitudinal slits. Fruits slenderly pedicellate, relatively thin-walled, more or less polished and mottled, subglobular-urceolate with a thin, sharp, usually conspicuously spreading rim above a very short, broad neck, mostly 1-1.5 cm. long and 0.8-1.2 cm. wide, rarely somewhat smaller and rarely up to 2 cm. long and 1.5 cm. wide; valves deeply enclosed, commonly 4. Seeds with a long terminal wing.

NORTHERN TERRITORY.—Near (NW. of) Katherine, open *Eucalyptus* forest, stony, hard soil, about 180 m., locally dominant, 20.vi.1946, *Blake* 16030; Katherine Gorge, 14° 19′ S., 132° 25′ E., rocky hillcrests with *E. phoenicea*, 183-186 m., 13.x.1946, *Blake* 17210; 7 miles S. of Pine Creek, slopes on granite, 29.viii.1948, *Perry* 1944; SE. of Alexandria Station, 19° 10′ S., 136° 47′ E., low, open mixed scrub on stony ridge, 296 m., 22.v.1947, *Blake* 17918; 8 miles NW. of Tennant Creek, alluvial soil near creek, 25.viii.1948, *Perry* 586. QUEENSLAND.—Burke district: Barkly Downs Station, 20° 21′-43′ S., 138° 24′-35′ E., on *Triodia*-clad, sandstone-quartzite rocky ridge, 268 m., 27.v.1947, *Blake* 17946.

Types.—Lectotype of *E. dichromophloia*: in rocks of the Fitzmaurice Ranges, Oct. 1855, *F. Mueller* (MEL, NSW); figured in Maiden, Crit. Rev. *Eucalyptus* 4: Plate 165, Figure 5, and in this paper, Plate 15.

Lectotype of *E. niphophloia*: *Jacobs* 82 from W. of Pine Creek (NSW, AFSC, BRI), figured in Plate 16.

Holotype of *E. erythrophloia*: The old battery, Eidsvold, Queensland, *Bancroft* (NSW); figured in Maiden, op. cit., 5: Plate 202, Figure 3.

Holotype of *E. arenaria*: *Gardner* 1501 from King Edward River, W. Australia (NSW).

Type of *E. polycarpa* var. *oligocarpa*: *Jacobs* 168 from Alice Springs (NSW, AFSC, BRI).

Widely spread across northern Australia, extending S. to within the region of the 10-in. isohyet in Western Australia and South Australia (map 11).*

The characters that together chiefly distinguish this species are the usually narrow leaves only slightly paler on the lower surface; the small, more or less rounded, usually quite smooth buds abruptly contracted to their slender but short pedicels; the thin-walled, subglobosely urceolate, more or less polished and mottled fruits; the seeds with a long terminal wing; and the non-peltate juvenile leaves pubescent beneath.

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* This species has not previously been recorded from South Australia. The record is based on the following collections:

South Australia.—Everard Range, Apr. 1950, *Cleland* (brown, rough bark) — *b., fl.;* Mt. Woodroffe, 18.iv.1950, *Cleland* — *fr.;* foot of Mt. Woodroffe, Apr. 1950, *Cleland* — *fr.*

E. dichromophloia is represented at Melbourne by three collections collected and labelled by Mueller. Maiden, who saw only fragments of the Melbourne material, arbitrarily treated a specimen from the Roper River* as the type and a specimen from the Fitzmaurice River as a "co-type". But this specimen from the Fitzmaurice River is the most satisfactory of the three (all are scrappy), and the label has the notes on the habit and bark published in the protologue; it seems to me to be the natural choice for the lectotype. All three evidently represent one and the same species, and, so far as scrappy material is comparable, look very much alike.

E. niphophloia was founded on specimens collected by Jensen and by Jacobs, but no type was indicated. Only *Jacobs* 82 and 108 were cited in the protologue, although Jacobs collected several other numbers written up by him as *E. niphophloia*. *Jacobs* 82, in bud, old flower, and fruit and with bark, is a good representative collection and the Sydney sheet is marked TYPE. This sheet is labelled as coming from Burrundie, but Jacobs's own labels are marked "W. of Pine Creek". This number is accepted as the type collection.

E. dichromophloia was said to differ from *E. niphophloia* in having discolorous leaves with a closer and more finely reticulate venation, but I can find no difference in these or any other features on the type material. On the whole, the leaves of the specimens referred by Blakely and Jacobs to *E. niphophloia* are rather broader than of those they referred to *E. dichromophloia*, but there is considerable variation on some specimens, and one of the three leaves on the lectotype of *E. dichromophloia* is broader than some of those on the type collection of *E. niphophloia* (cf. Plates 15, 16, but note the difference in the scale). The leaves on the type collection of *E. niphophloia* are now slightly, though distinctly, paler on the lower surface, and the impression gained from the occasional re-examination of *Blake* 16030 during the past three years is that any slight difference between the colour of the two surfaces tends to become exaggerated after the specimens have been dry for a year or more, and the venation then becomes slightly more prominent.

The type of *E. erythrophloia* consists of abundant material. At first sight it looks different because of the large fruits up to 2 cm. long, but much of the other material from Queensland determined by Blakely as belonging to this species is intermediate between the type and the syntypes of *E. niphophloia* and *E. dichromophloia*. Blakely stressed certain alleged differences in the bark of these three forms. *E. dichromophloia* was originally described as having whitish, smooth bark that at length broke up and slowly shed from the reddish inner bark; the result would be that some reddish and scaly bark would be present, at least during part of the time the bark remained on the tree, and this is also the state described for *E. niphophloia.* The degree of persistence of the old bark varies considerably; when the shedding is very slow, the bark tends to be scaly and more or less mottled reddish and whitish. Occasionally this mottled scaliness persists over a large part of the tree and may attain sufficient thickness, particularly towards the base, to give a more or less tessellated appearance (cf. *Blake* 17210); this is the state described for *E. erythrophloia* and it is common in eastern Queensland. Parallel variations in the bark occur in *E. terminalis, E. latifolia,* and *E. foelscheana.*

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* The locality given on the label is "Tableland and rocky plains, sources of the Roper, 23-24.7.56." On these dates, Mueller was about SE. of and not far from the site of the present homestead of Hodgson Downs.

E. arenaria was described from a single collection, from trees with rough, flaky, reddish black or dark grey bark on the trunk, reddish in fracture. The fruits have a slightly longer neck than is usual in *E. dichromophloia,* but an intermediate state is found in *Blake* 17210 with rather similar bark. The angular twigs stressed by Blakely are frequent in *E. dichromophloia.*

Some specimens referred to *E. polycarpa* by Blakely and Jacobs belong here. *E. polycarpa* var. *oligocarpa* represents an extreme form of shrubby habit with reduced inflorescences; comparable states of *E. terminalis* are to be found, but shrubby states may also occur without greatly reduced inflorescences as represented by *Blake* 17946.

Although long and narrow adult leaves seem to be characteristic for the species, shorter and broader leaves (sometimes only about three times as long as wide) are not uncommon (see Fig. 2); in herbarium material they seem to be always associated with narrower ones. These broad leaves sometimes resemble the narrower ones of *E. latifolia,* which has the intramarginal vein always very close to the margin, but in *E. dichromophloia,* increasing breadth of leaf is associated with an increasing distance between the intramarginal vein and the margin (see Fig. 3). It seems likely that these broader leaves are comparable with intermediate leaves, but they are to be found on twigs that are not obviously reversion shoots. The juvenile leaves have not previously been described in detail; the pubescent lower surface is remarkable, and is rather similar to the state of affairs in *E. jacobsiana.*

In the adult state, *E. dichromophloia* resembles *E. latifolia* more than any other species. From this it differs in the narrow leaves (see previous paragraph) and in the more distinct neck and the expanded rim of the usually mottled fruit.

E. dichromophloia is also close to *E. terminalis,* but differs from it in that the midrib is usually rather deeply impressed on the upper surface of the leaf, which is usually narrower and more acute; the smaller and plumper buds are rather more abruptly contracted to their pedicels and are usually reddish and more or less shining (not white, cream, or scurfy); and the fruits are (on the whole) shorter, plumper, always with thinner

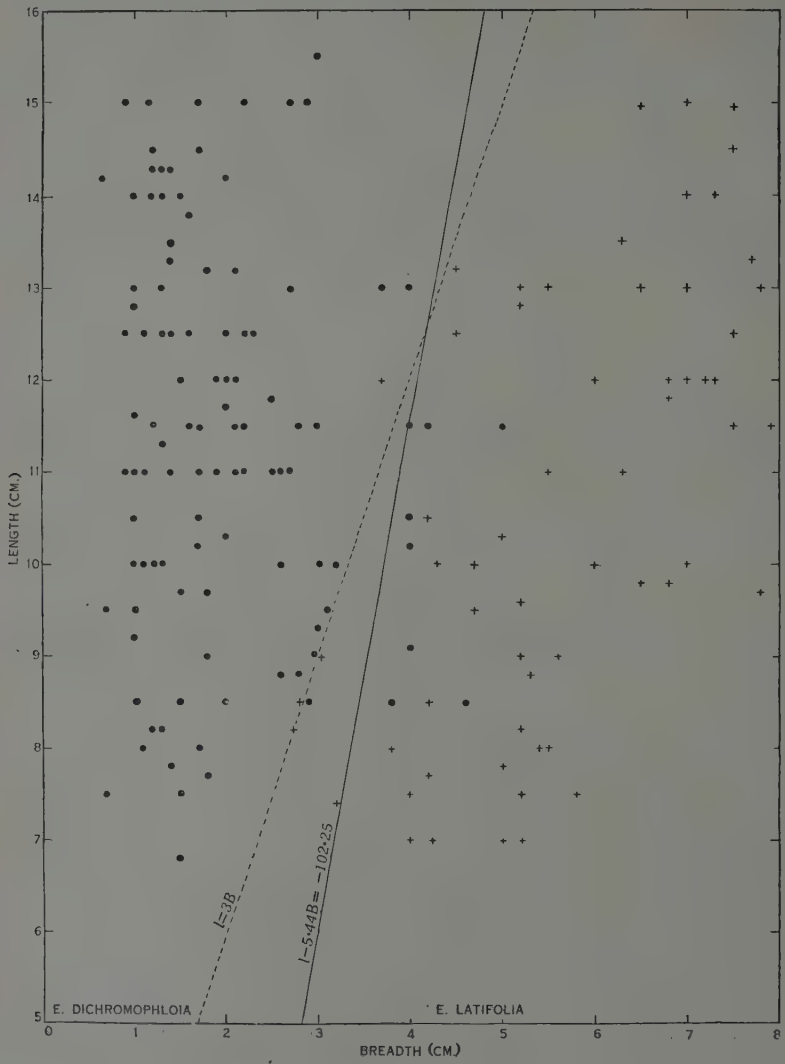

Fig. 2.—Scatter diagram showing the relation between actual length and breadth of leaf in *E. dichromophloia* (towards the left) and *E. latifolia* (towards the right). The points to the left of the broken line indicate leaves more than three times as long as wide, those to the right indicate leaves less than three times as long as wide. The full line is the line represented by the equation $l - 5.44B = -102.25$, which gives a sharper line of discrimination (see Appendix I).

walls, and commonly with an acutely edged, thin, expanded rim. Some specimens from Central Australia are particularly difficult to distinguish from *E. terminalis;* some (e.g. *Perry* 586) even have pruinose or somewhat scurfy buds, but they are more abruptly narrowed to the pedicel and smaller than in *E. terminalis*, while the fruits have thinner walls with acute and more spreading rims.

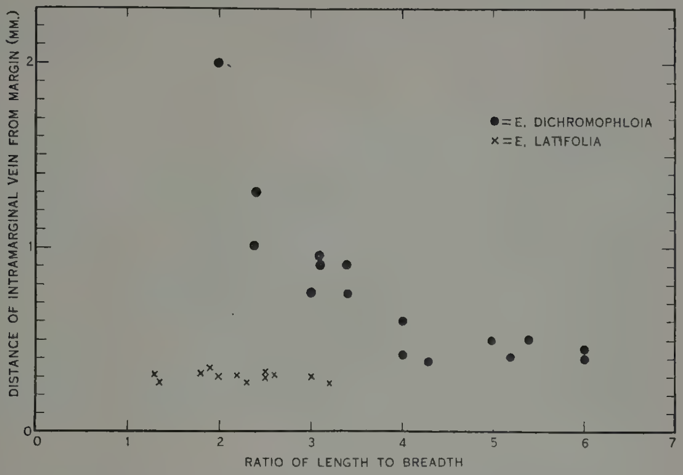

Fig. 3.—Relation between relative breadth of leaf and the distance of the intramarginal vein from the margin in *E. dichromophloia* (above) and *E. latifolia* (below). When the length: breadth ratios for the two species overlap there is a big difference in the distance between the margin and the vein. Based on *Blake* 16030 and *Jacobs* 70*A* for *E. dichromophloia* and *Blake* 16077*A* and *Blake* 17044 for *E. latifolia.*

19. **Eucalyptus latifolia** F. Muell. in J. Linn. Soc. (Bot.) 3: 94 (1859); non Hollick (1906)

More or less deciduous tree up to about 12 m. high; bark on the lower part and sometimes almost throughout scaly, reddish and grey, and persistent, elsewhere smooth, white or nearly so, and deciduous. Juvenile leaves shortly petiolate, orbicular-ovate to elliptic-ovate, rounded and apiculate at the apex, almost rounded at the base, neither cordate nor peltate, with the intramarginal vein very close to the margin, more or less setose, at least on the midrib beneath; petioles and stem likewise setose. Intermediate leaves prominently petiolate, nearly opposite, broadly ovate, very obtuse, abruptly narrowed to the petiole or truncate or even subcordate at the base, up to 13.5 × 13 cm. Adult leaves alternate or subopposite, long-petiolate, concolorous, mostly broadly ovate to orbicular-ovate but sometimes more or less oblong, mostly 7-15 cm. long and 3-9.5 cm. wide, mostly 1.5-2 (rarely up to about 3) times as long as wide, with the intramarginal vein contiguous to the margin and 30-50 pairs of lateral veins at an angle of 50°-65° with the midrib; petioles 1.8-4 cm. long. Panicles terminal or also subterminal, sometimes pyramidal rather than corymbose; pedicels about 3-6 mm. long. Buds rounded, abruptly contracted to their pedicels, about 5-6 mm. long and 4-5 mm. wide. Anthers obovate-oblong, versatile, with parallel cells opening in longitudinal slits. Fruit pedicellate, smooth, ovoid-globular with a scarcely distinct neck and a narrow, scarcely expanded rim, rarely noticeably longer than wide, from 9 mm. long and 8 mm. wide up to 15 mm. long and 14 mm. wide, with the orifice 4-6 mm. wide and 3 or 4 deeply enclosed valves. Seeds with a long terminal wing.

NORTHERN TERRITORY.—Near Margaret R., in about 13° 6′ S., and 131° 22′ E., alluvial flat, hard, grey soil, alt. about 30 m., 17.ix.1946, *Blake* 17044; about SSE. of mouth of Daly R., 13° 51′-53′ S., 130° 20′-30′ E., locally dominant in mixed open forest, about 34 m., 25.vii.1946, *Blake* 16617; near Edith R., NW. of Katherine, in open *Eucalyptus* forest, stony, hard soil, 24.vi.1946, *Blake* 16077*A*; 20 miles SE. of Katherine, gravelly lateritic podsol, 26.viii.1948, *Perry* 1936; 30 miles ENE. of Bradshaw Station, dominant tree on alluvial yellow podsol, 20.viii.1949, *Perry* 2706.

Type.—Near the junction of Dry R., King R., and Darrinyan Creek, 8.vii.1856, *F. Mueller* (MEL) (Plate 17); Mueller's field label reads "Upper part of the Roper River 8. Jul. 56.", but his position at the date shown was as given above.

Rather widely spread in the northern part of the Northern Territory and the adjacent parts of Western Australia, chiefly on flats and the lower slopes (map 10).

By reason of its broad leaves and bark varying from smooth and whitish nearly throughout to scaly and reddish and grey nearly throughout it resembles *E. foelscheana;* it differs from this species in that the buds are much smaller, more rounded in outline, and abruptly contracted to their pedicels, and in the very much smaller fruits nearly as wide as long with at most a very short neck. It is very close to *E. dichromophloia* from which it differs in the broader leaves and the scarcely expanded rim of the fruit. Only very rarely are the leaves of *E. latifolia* more than three times as long as wide and only very rarely are the leaves of *E. dichromophloia* so wide as this. The intramarginal vein in *E. latifolia* is always more or less confluent with the margin; it is confluent with the margin in the narrower leaves of *E. dichromophloia,* but in the broader leaves this vein is quite distinct from the margin, with the distance between them increasing with the width of the leaf. See also the discussion under *E. dichromophloia* and Figures 2 and 3.

In foliage, *E. latifolia* somewhat closely resembles *E. bigalerita* and *E. oligantha,* but the more numerous lateral veins and the intramarginal vein so close to the edge readily distinguish it from these species. The habit and bark are shown in Plate 1, Figure 2, and Plate 8.

Mueller described the fruit as being 3 lines long with a slightly reflexed rim; this is true for those of the type, but they are very immature. Mueller also described the leaves as 2-3 in. long, but the smallest leaf on the type is 6 cm. long and this is imperfectly developed at the apex.

E. latifolia Hollick was based on a fossil leaf impression from America; it bears no relation to the living plant known by this name, and it is very doubtful if the impression represents a eucalypt at all.

20. **Eucalyptus foelscheana** F. Muell. in Melb. Chemist and Druggist 55: 56 (1882)

E. leiophloia Blakely & Jacobs in Blakely, Key Eucalypts 82 (1934).

E. leiophloia Blakely & Jacobs var. *lepidophloia* Blakely & Jacobs in Blakely, Key Eucalypts 83.

Tree to 10 m. high, but often small and scrubby, and bushes have been found in flower and fruit when only 45 cm. high; twigs stiff, rather stout, terete. Bark on the taller trees for the greater part smooth, white or whitish, and deciduous, with some more or less persistent, scaly, rusty or mottled bark near the base; on small trees this rusty, scaly bark often extends over the greater part of the tree and sometimes throughout. Juvenile leaves opposite for a few pairs, shortly petiolate, ovate, not peltate, very sparsely setose chiefly on the midrib beneath. Intermediate leaves broadly ovate or ovate-oblong, often very large, up to at least 26 × 20 cm. Adult leaves hard, concolorous, often more or less yellowish, alternate, on petioles 2-3 cm. long, varying from ovate and acute or elliptic to broadly ovate or orbicular and then very obtuse, abruptly rounded at the base to somewhat cuneate or somewhat cordate, 1.3-2.1 times (mostly less than twice) as long as wide, mostly 11-18 cm. long and 6-12 cm. wide, with 30-36 pairs of lateral veins at an angle of 50°-80° with the midrib, and the intramarginal vein confluent with the margin. Inflorescence a relatively small corymbose panicle smaller than the leaves and sometimes reduced to very few flowers. Buds pallid or reddish but not conspicuously scurfy, pyriform-obovoid, gradually narrowed to a pedicel about as long as the calyx-tube, about 1.2-1.4 cm. long and 0.7-1.1 cm. wide; operculum narrower than the calyx-tube and one-quarter to one-third as long as it, more or less conical and sometimes umbonate. Anthers versatile, obovate-oblong, with parallel cells opening in longitudinal slits. Fruits thick and woody on relatively slender pedicels 5-15 mm. long, urceolate to truncately ovoid or obpyriform, mostly 2-2.6 cm. long and 1.6-2 cm. wide; valves 4, rarely 5, very deeply enclosed. Seeds with a long terminal wing.

WESTERN AUSTRALIA.—Five miles E. of Kimberley Research Station, Ord. R., open forest on very deep sand, 23.vii.1949, *Perry* 2567. NORTHERN TERRITORY.—Near Manton Dam, 12° 53′ S., 131° 5′ E., occasional in open community of *Eucalyptus papuana* on lower part of gentle slope with podsolized soil, about 45 m., 18.viii.1946, *Blake* 16805; near Margaret R., about 13° 8′ S., 131° 20′ E., with *E. clavigera* and *Xanthostemon paradoxus* on low ridge, light grey lateritic soil, about 40 m., 27.ix.1946, *Blake* 17081; E. of mouth of Daly R., 13° 21′ S., 130° 36′ E., co-dominant with *E. confertiflora* over large areas with pale grey, hard soil, 71 m., or locally dominant, 30.vii.1946, *Blake* 16672; near Brocks Creek, in *Eucalyptus* forest on stony hills, about 145 m., 26.vi.1946, *Blake* 16137; near Brocks Creek, gentle slope with grey podsol, "orchard country", co-dominant with dwarf trees of *E. confertiflora*, 92 m., 25.vi.1946, *Blake* 16108; near Cullen Siding, 14° 1′ S., 131° 54′ E., common in mixed open *Eucalyptus* forest, grey, sandy soil, 162 m., 23.x.1946, *Blake* 17290; Katherine, 25.vii.1947, *Perry* 416; 20 miles SW. of Katherine, levee near King R., 3.vi.1949, *Perry* 1988.

Types.—Syntypes of *E. foelscheana*: north of Arnhem Land, *McKinlay* (MEL); without definite locality, *Foelsche* (MEL). Mueller's plate in "Eucalyptographia" was drawn from these, except the leaf in the bottom right-hand corner. See also Plates 18 and 19 of this paper.

Lectotype of *E. leiophloia*: *Jensen* 417 from Umbrawarra (NSW); Plate 20; lectoparatype: *Jensen* 420 from Woolngi (NSW).

Type of *E. leiophloia* var. *lepidophloia*: *Jacobs* 71 from slopes from Stapleton to Daly R. (NSW, AFSC, BRI); Plate 21.

Widely distributed in the northern part of the Northern Territory and adjacent parts of Western Australia (map 6), sometimes occurring alone, sometimes associated with *E. clavigera* or *E. confertiflora,* while sometimes it occurs in mixed open forest. The trees are commonly deciduous for part of the dry season.

In foliage and habit *E. foelscheana* sometimes resembles *E. latifolia* so closely as to be indistinguishable from it in the absence of buds, flowers, or fruit, all of which are very much larger in *E. foelscheana* and rather different in shape. Except for the broad leaves, it also resembles *E. terminalis* but the buds are nearly or quite smooth with the operculum distinctly narrower than the calyx-tube, and the fruits are more usually reddish and somewhat shining with a less obtuse rim. Habit and bark are shown in Plate 4, Figure 2; Plate 5, Figure 1; and Plate 2, Figure 2 (*c*).

E. foelscheana was described from two collections. One of these consists of two loose leaves and two loose fruits with seeds collected by Paul Foelsche and is not definitely localized. The other is a good sheet of two pieces in bud and flower with a packet containing pieces of an inflorescence, loose buds and flowers, an entire unripe fruit, and a similarly unripe fruit sectioned vertically; according to the label written up by Mueller, the specimen was collected by J. McKinlay (cited as M'Kinlay by Mueller) "North of Arnhems Land", possibly in the neighbourhood of Anson Bay, after his unfortunate expedition of 1865 from Escape Cliffs to the East Alligator River. Accompanying Foelsche's specimen is Mueller's MS. of the article of which the original description formed part, and also a typewritten translation of a letter from Foelsche to Mueller, dated "Port Darwin, 19th September, 1882". The pertinent passage in this letter reads:

"I thought I had given you a description of the Eucalypt which I considered to be *E. grandifolia* and which you called *E. Foelscheana* in my honour. The young plant when 15″ to 18″ high gets a bunch of buds as large as a fist on top which open up into large white flowers. If I am not mistaken I sent you, together with the leaves, some green fruit. The grown up trees, as far as I noticed, reach a height of up to 20′ and look yellowish (?) ;* and are seldom more than 9″ thick. They have dark rough bark and the leaves are about half as big as those I sent you. The tree grows in a meagre sandy soil and the wood can only serve as fuel. — I shall try to obtain flowers and ripe fruits when the time comes".

It is evident that Mueller made use of both Foelsche's letter and McKinlay's specimen in drawing up the description. In the following year Mueller figured the species in Eucalyptographia, dec. 9. He repeated the protologue with a few minor changes, but added dimensions of the organs described. The spelling of McKinlay's name was corrected, and a specimen of Burkitt's from Bridge Creek was also cited. In both publications specimens collected by R. Brown were tentatively referred to the species.

It has been presumed that Foelsche's specimen came from the immediate vicinity of Port Darwin (cf. Maiden, op. cit., 5: 4-5 (1920)), although according to Jensen, ex Maiden (loc. cit., 6) and in Ewart and Davies, Fl. North. Territ. 313, Foelsche collected the material in the neighbourhood of Brocks Creek and Bridge Creek. Maiden (loc. cit., 4) took the figure in the Eucalyptographia as representing the type, but the figure appears to have been drawn from at least three collections. The central portion of the figure, representing a twig in flower and fruit, is most like McKinlay's specimen (cf. Plate 18), but some "reconstruction" appears to have been undertaken by the artist to include the fruiting panicle on the same twig. There is a fruit in vertical section in the packet on the McKinlay sheet from which Figure 7 may well have been drawn. The large leaf behind the central twig is an exact representation of one of the leaves collected by Foelsche (cf. Plate 19), and the seeds were probably drawn from the same collection; the narrow leaf towards the lower right-hand corner of the plate was evidently drawn from Brown's collection.

From Foelsche's letter, it is evident that the leaves sent to Mueller are intermediate leaves. There is no doubt that both the collections of Foelsche and McKinlay represent one and the same species, and for all practical purposes, it might be as well to continue to treat the two as syntypes. Some may prefer to typify the species on Foelsche's specimen alone because of the specific epithet chosen by Mueller, but against this it must be stressed that nearly all the important taxonomic characters in the description could *only* have been taken from McKinlay's specimen, such as the arrangement of the leaves, structure of the inflorescence, the buds, operculum, and anthers, while the description of the fruits and seeds could have been as well drawn from McKinlay's specimen as from Foelsche's. If a decision on a single lectotype is necessary, then McKinlay's specimen would be the logical choice.

E. leiophloia was based on specimens collected by Jacobs and by Jensen from trees with — for the most part — smooth, white bark and "lanceolate" to ovate-lanceolate leaves. No type was indicated in the protologue. There is a quotation of a generalized statement by Jacobs, and this is followed by a citation of some of Jensen's collections and field observations. Owing chiefly to faulty punctuation, the references to Jensen's specimens are vague and misleading. At least four collections are involved — Umbrawarra, *Jensen* 416; Umbrawarra, *Jensen* 417; Cullen River (and Woolngi), *Jensen* 419; and Woolngi, *Jensen* 420. The field observations are not printed in full; they are attached to the sheet of 417, but they refer to 417, 418, 419, and 420. *Jensen* 418 has smaller fruits than those described and need not be considered in typifying the name. *Jensen* 416, 417, and 420 are all marked TYPE. The fruits of *Jensen* 416 are not urceolate and so do not conform to the description. *Jensen* 417 (in fruit) and *Jensen* 420 (in bud and flower and also with intermediate leaves) are selected here as lectotype (cf. Plate 20) and lectoparatype respectively; the selection of a paratype seems desirable, as the description refers to both flowers and fruit and both stages are not present on any one specimen.

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* The query is possibly the translator's. The trees of this species do look yellowish.

E. leiophloia var. *lepidophloia* was based on specimens from small, crooked trees with scaly bark, broad, coarse leaves "12-20 × 6-15 cm." and urceolate fruits. Spencer's specimens from "Track to Katherine River, and Katherine River" were quoted as the type; *Jacobs* 71 with field observations was also quoted and (by implication — the locality only was cited) *Hill* 450, 452, 455. Two collections are covered by the phrase just mentioned, but neither agrees with the description. They are figured in Maiden, loc. cit., Plate 169, Figures 1, 2, and 6. The specimen from "Track to Katherine River" (Fig. 6) has leaves only 8-11 cm. long and 2.5-6 cm. wide, while the fruits of the collection from "Katherine River" (Figs. 1-2) are not urceolate and rather small. At Sydney, Jacobs's specimen is marked TYPE; this agrees with the description, and since the variety is based largely on habit and bark (characters not described by Spencer) it seems that this is correct and that some error occurred in the protologue. The leaves of *Jacobs* 71 are very similar to those on McKinlay's specimen discussed earlier; the resemblance between these collections is much closer than a comparison of Plates 21 and 18 would suggest.

From the descriptions and data concerning habit and habitat given by Jacobs, it was easy in the field to recognize *E. leiophloia* and *E. leiophloia* var. *lepidophloia*. Doubts were aroused when it was noticed that the original description of *E. foelscheana* quoted by Jacobs also precisely described *E. leiophloia* var. *lepidophloia*. Field observations extending over some months led to the conviction that *E. leiophloia* and *E. leiophloia* var. *lepidophloia* were states of one and the same species, differing only in height and the not always correlated amount of smooth bark. Large trees sometimes have smooth bark almost to the base; small trees usually have scaly bark extending to the branches. *E. foelscheana* was based, at least in part, on specimens from small trees, and Foelsche's description of the tree agrees with that of Jacobs. An examination of the type material of the three names confirmed that all referred to the same species.

Maiden, op. cit., 5: 4-5 (1920) had noted forms of *E. foelscheana* with narrower leaves than the type, and Blakely seems to have regarded the narrow leaves as normal for the species. In a sense he was right, for well-grown trees often do produce a large proportion of narrowly ovate leaves. However, some confusion arose with another form collected by Jacobs (and earlier by Allen, Hill, and Holtze) in the neighbourhood of Darwin with leaves very like these narrower leaves of *E. foelscheana*, but with different bark, buds, and fruits; and it was chiefly for this form (form 1 of Maiden) that Blakely and Jacobs used the name *E. foelscheana*, while the names *E. leiophloia* and *E. leiophloia* var. *lepidophloia* were proposed for the broader-leaved forms. The narrower-leaved "Form 1" appears to be an unnamed species; it is described below under the name of *E. porrecta*.

21. **Eucalyptus porrecta** S. T. Blake; sp. nov. cum *E. foelscheana* F. Muell. prius confusa, sed ab hac cortice omnino rimoso sursum neque squamoso neque laevi, foliis pro more conspicue angustioribus, pedicellis longioribus gracilioribusque, alabastris turgidioribus conspicue rugosis et eorum operculo cum tubo calycis subaequilato, fructibus latioribus ovoideis vel subglobosis apicem versus gradatim angustatis nec constrictis, distinguenda.

Arbor glabra, usque ad 3.5 m. alta, cortice rugoso rimoso plus minusve tessellato griseo usque ad ramulis novellis obtecta. Ramuli teretes. Folia adulta alterna, petiolata, concoloria vel fere concoloria, opaca; petioli 1.8-2.5 cm. longi; laminae lanceolatae vel late lanceolatae, acutae vel acute acuminatae, plus minusve apiculatae, pro more 10-23 cm. longae et 3-7.5 cm. latae, bis vel ter vel fere quater longiores quam latae; costa utrinque admodum elevata etiam pro majore parte canaliculata; nervus intramarginalis praecipue basin versus cum marginibus incrassatis confluens; nervi laterales circiter 30-40 utrinsecus costam et cum ea angulum 50°-60° facientes. Inflorescentia terminalis, corymboso-paniculata, folia pro more superans; umbellae 3-7-florae; pedicelli graciles, pro more angulati, sursum minime incrassati, sub anthesi plerumque 1.2-2 cm. longi, sub fructu subsimiles. Alabastri rufescentes, conspicue rugosi, haud squamosi, a pedicello distincti sed in eum gradatim angustati, circa 1.3-1.5 cm. longi, 1-1.2 cm. lati; tubus calycis obconicus, 1.0-1.2 cm. longus, aequilatus; operculum late conicum, tubo calycis subaequilatum sed brevius, ab eo irregulariter circumscissum. Stamina permulta, circa 1.2 cm. longa; antherae versatiles, oblongo-obovatae, earum loculi paralleli in rimos longitudinales dehiscentes, ad connectivum glandem dorsalem gerentes. Fructus ovoidei vel subglobosi, truncati, vix vel minime urceolati, in pedicellum abrupte contracti, margine angusto circa 1.5 mm. crassi, ore 8-9 mm. lati, in toto 2-2.5 cm. longi fere aequilati (1.7-2 cm. lati), 4-5-loculati; valvae profunde inclusae; semina ala longa terminata.

Tree, quite glabrous, up to 3.5 m. high, with grey, more or less tessellately scaly bark up to the small branches. Branchlets terete. Adult leaves alternate, petiolate, concolorous or nearly so, dull; petiole 1.8-2.5 cm. long; blades lanceolate to broadly lanceolate, acute or acutely acuminate, more or less apiculate, mostly 10-23 cm. long and 3-7.5 cm. wide, mostly 2-3.5 times or rarely up to 4 times as long as wide; midrib slightly elevated on both sides but channelled nearly throughout; intramarginal vein more or less confluent with the thickened margin, particularly towards the base; lateral veins in about 30-40 pairs, at an angle of 50°-60° with the midrib. Inflorescence a terminal corymbose panicle, mostly exceeding the leaves; umbels 3-7-flowered; pedicels slender, more or less angular, not much thickened upwards, 1.2-2 cm. long in flower and as long or more usually longer than the buds, scarcely altered in fruit. Buds reddish, conspicuously rugose, not at all scurfy, gradually narrowed to the pedicel but sharply distinct therefrom, about 1.3-1.5 cm. long, 1.0-1.2 cm. wide; calyx-tube obconic, 1-1.2 cm. long and wide; operculum broadly conical, about as wide as the calyx-tube but shorter, irregularly circumsciss. Stamens numerous, about 1.2 cm. long; anthers versatile, oblong-obovate, with parallel cells opening in longitudinal slits and with a large dorsal gland. Fruit ovoid or subglobose, truncate, abruptly contracted to the pedicel, scarcely if at all urceolate, the rim narrow, about 1.5 mm. thick, the orifice 8-9 mm. wide, in all 2-2.5 cm. long and 1.7-2 cm. wide; valves 4 or 5, very deeply enclosed; seeds with a large, terminal, membranous wing.

NORTHERN TERRITORY.—Melville Island, 27.vi.1933, *Jacobs* 27, 30; Shoal Bay Road, 14 miles from Darwin, 5.xi.1933, *Allen B*28 (small tree, rough, lightish grey bark persistent throughout trunk and branches; on flat, only very few trees, these stunted); Darwin, *Hill* 344 ("bloodwood"; rough bark on trunk and branches; small trees; flowers (about) July; capsules 25.x.1915); Darwin, *M. Holtze* 1257 in part (dark grey, rough bark throughout; small tree); Darwin, Nov. 1942, *Faux;* Darwin, 10.vii.1933, *Jacobs* 47; near "Koolpinyah", 12° 24′ S., 131° 10′ E., in *E. miniata-E. tetrodonta* tall forest on rubbly ironstone lateritic soil, 24 m., 8.ix.1946, *Blake* 16951 (small, slender tree of 3-3.5 m.; grey, more or less tessellately scaly bark up to small branches; light, somewhat olive-green leaves).

Type.—Blake 16951 (BRI, CANB, K, A, L, MEL, NSW); *paratype*: *M. Holtze* 1257 (MEL, BRI); both figured in Plate 22.

Known chiefly from the neighbourhood of Darwin (map 7*B*) this species is distinguished from its allies by the following combination of characters: rough, grey bark throughout; leaves about the same colour on both sides, neither particularly broad nor particularly narrow; long, slender pedicels; wrinkled, turgid buds, which are not scurfy; broad, rather large fruits without a distinct neck and with a thin and scarcely expanded rim. It has been confused with *E. foelscheana,* from which it differs in the entirely rough, grey bark; in the narrower and usually much longer, very acute, darker-coloured leaves with sulcate midrib and less oblique veins; longer, more slender pedicels usually longer than the buds (shorter than the buds in *E. foelscheana*) and up to as long as the fruit (rarely more than half as long as the fruit in *E. foelscheana*); plumper, wrinkled buds with the operculum about as wide as (not conspicuously narrower than) the calyx-tube; and in the broader fruit without a distinct neck. It differs from *E. terminalis* in bark and fruit in the same way as it does from *E. foelscheana;* moreover, the leaves are mostly larger, with fewer and more widely spaced veins and more depressed midrib; the plumper, wrinkled buds are not scurfy; and the pedicels are usually longer, more slender, and more angular. From *E. polycarpa,* which it resembles in the bark, it differs in general habit, in the larger leaves not conspicuously paler on the lower surface and with fewer and more widely spaced veins, in the longer pedicels, in the larger, wrinkled but not scurfy buds of different shape, and in the broadly rounded fruit. *E. bleeseri* has long, slender pedicels, but is otherwise very different. *E. cliftoniana* has broad fruits, but with much thicker walls; its leaves are much narrower with more numerous and more closely spaced lateral veins and are much thicker in texture and the pedicels are short.

The specimens cited above form a fairly homogeneous series. In *Jacobs* 27, one leaf is 5 times as long as wide and some in *Jacobs* 47 are about 4 times as long as wide. Some short pedicels, only 6 mm. long, are also present in *Jacobs* 47. A second sheet of *M. Holtze* 1257 (MEL) carries a fruiting specimen of *E. foelscheana.*

22. **Eucalyptus cliftoniana** W. V. Fitzg. in Maiden, Crit. Rev. *Eucalyptus* 4: 209 (1919)

Shrub or small tree up to 12 m. high, with rough, scaly or tessellated, mottled reddish and grey bark up to the twigs; twigs slender, terete or compressed. Adult leaves glabrous, alternate or opposite, concolorous, lanceolate and more or less falcate, acute or acutely acuminate, narrowed to the base, 8-14 cm. long, 1.1-2.6 cm. wide, 5-8 times as long as wide; midrib channelled on both surfaces; lateral veins slender and partly hidden in the thick texture of the leaf, in about 50-70 pairs at an angle of 60°-70° with the midrib; intramarginal vein more or less confluent with the thickened margin; petiole 0.8-1.2 cm. long. Fruiting pedicels very short or up to 6 mm. long, slender. Fruits thick and woody, subglobular or globular-oblate (as wide as or slightly wider than long), sometimes with a very short and indistinct neck, truncate, 1.5-2.5 cm. long, 2-2.5 cm. wide, with numerous very faint ribs; rim about 2 mm. wide, flat, or insloping and therefore acute; orifice 6-11 mm. wide; seeds with a long terminal wing.

NORTHERN TERRITORY.—WSW. of "Victoria River Downs", near junction of Gibbie Creek with Wickham R., flat-topped hill with *Plectrachne pungens* on sandy soil overlying sandstone, 18.vi.1949, *Perry* 2166. WESTERN AUSTRALIA.—Twenty miles S. of "Lissadel", steep, rocky, conglomerate slope, 3.viii.1949, *Perry* 2677.

Type.—Mount Anderson and Grant Range, Western Australia, August 1906, *W. V. Fitzgerald* (NSW); figured in Maiden, loc. cit., Plate 157, Figure 4.

Known to me only from the material cited above, which consists entirely of specimens with adult leaves and mature fruits. The most distinctive character is the very broad, woody fruits on short but slender pedicels; the leaves resemble those on some specimens of *E. terminalis* and *E. dichromophloia,* but are smaller. According to Perry (in conversation) the bark resembles that on the lower part of the trunk in *E. terminalis;* there is no smooth bark on the upper part (map 7*E*).

23. **Eucalyptus ptychocarpa** F. Muell. in J. Linn. Soc. (Bot.) 3: 90 (1859)

Spreading tree with drooping branchlets and grey, compactly fibrous, brittle, and more or less tessellately fissured bark. Juvenile leaves more or less rounded to elliptic, petiolate, glabrous, cuspidate or retuse. Intermediate leaves alternate, becoming broadly lanceolate, more or less peltate, up to 40 × 17 cm. Adult leaves markedly paler beneath, alternate or here and there opposite, petiolate, narrowly ovate to lanceolate, acute or acuminate and more or less caudate, rounded at the base and sometimes distinctly peltate, 23-35 cm. long, 6-14 cm. wide, 2-4 times as long as wide, with a large number (60-80 pairs) of lateral veins at an angle of 65°-75° with the midrib; petioles 2-3 cm. long. Inflorescence a terminal corymbose panicle shorter than the leaves, sometimes reduced to a few flowers; umbels about 5-flowered; pedicels relatively slender and not much thickened upwards, 1.5-2.2 cm. long. Buds obovoid, more or less acute, sharply distinct from the pedicels, with 9-12 prominent ribs, 2-2.3 cm. long and 1.7-2 cm. wide; operculum about half as long as the calyx-tube or rather more, more or less pyramidal. Anthers versatile, obovate-oblong, with a dorsal gland and parallel cells opening in longitudinal slits; filaments red or white. Fruit woody, oblong or barrel-shaped, slightly incurved at the thick rim and sometimes shortly narrowed below it, with 9-12 more or less prominent ribs, about 3.5-4.5 cm. long and 2.7-3.5 cm. wide, the 4- or 5-celled capsule very deeply enclosed; seeds obliquely ovate, biconvex, with a long terminal wing, in all 13-16 mm. long and 4-5 mm. wide.

WESTERN AUSTRALIA.—Twenty-five miles NNE. of Argyle Station, on sandy soil near spring, 1.viii.1949, *Perry* 2665. NORTHERN TERRITORY.—About SSE. of Adelaide River, 13° 30′ S., 131° 8′ E., creek flat, 64 m., 6.ix.1946, *Blake* 16943; branch of Hayes Creek, 13° 38½′ S., 131° 26′ E., outside edge of fringing forest near a spring, about 105 m., 10.vii.1946, *Blake* 16402.

Type.—"Gulf of Carpentaria", 22.vii.1856. *F. Mueller* (K, photo in BRI). On this date Mueller was about NE. of the position of the present homestead of Nutwood Downs.

This species is distributed over parts of the Kimberley Division of Western Australia and the more northern parts of the Northern Territory and is usually found on low banks of streams and around springs (map 9).

The large leaves sometimes peltate even on the flowering twigs, large ribbed buds, very large, very woody, and strongly ribbed fruits, and long slender pedicels give a most distinctive combination of characters. The fruits often resemble some of those of *E. miniata*, but they are frequently five-celled, have long pedicels, and are borne in terminal inflorescences. The flowers are usually red, but occasional trees produce white flowers (one such was observed when *Blake* 16943 was collected). Sometimes the characteristic ribs on the fruit disappear, to judge from *Specht* 1121 from Oenpelli. The fruits accompanying this number are somewhat variable, but are rather severely weathered; some have distinct ribs, but in others the ribs have more or less completely disappeared. Some of the fruits in this collection are the smallest so far seen, as small as 3 cm. long and 2.2 cm. wide, but though evidently picked up from the ground, they may not be quite normal and were not considered in drawing up the above description. The peltate leaves on the flowering twigs are a peculiar feature. Blakely has completely ignored the presence of peltate leaves in the species — possibly because they appear not to occur among the early juvenile leaves — and has associated the species with those that do not produce peltate leaves.

The specimen at Kew quoted as the type is the only one collected (and labelled) by Mueller that has been found.

24. **Eucalyptus jacobsiana** Blakely, Key Eucalypts 92 (1934)

Tree 6-9 m. high with persistent, somewhat yellowish, fibrous, rather soft bark; twigs slender and angular. Juvenile leaves opposite or approximated in pairs for several pairs, linear to somewhat lanceolate, acute or cuspidate at the tip, decurrent at the base, subsessile to very shortly pedicellate, finely venulose on both sides with numerous lateral veins and rather prominent reticulations between, revolute at the margins, dark green and glabrous above, shortly and densely white-tomentose on the lower surface with short but broad and blunt reddish setae on the midrib and with scattered papilliform glands, which later disappear under the indumentum, from 2.5 cm. long and 0.2 cm. wide up to about 8 cm. long and 0.5 cm. wide; stems densely reddish-setose and also more or less closely glandular towards the tips. Intermediate leaves broader, up to 10 cm. long and 1.3 cm. wide, not distinctly glandular, but still whitish-tomentose beneath and with more or less revolute margins. Adult leaves alternate, petiolate, glabrous, lanceolate or narrowly lanceolate, gradually and acutely acuminate, tapering at the base to a petiole 0.5-1.2 cm. long, mostly 6-9 cm. long and 0.8-1.4 cm. wide, about 4.5-8 times as long as wide, upper surface green, more or less shining and indistinctly veined, lower surface pallid, dull, finely and closely veined with a large number (about 40 pairs or more) of lateral veins at an angle of 60°-70° with the midrib and closely reticulate between; intramarginal vein contiguous to the margin. Inflorescence a terminal corymbose panicle, sometimes with a few leaves near the base, sometimes becoming lateral in fruit. Buds broadly obovoid, obtuse, about 4-5 mm. long and 3 mm. wide, shorter than the filiform pedicels; operculum very short, nearly flat. Anthers versatile, obovoid-oblong, with parallel cells opening in longitudinal slits. Fruit broadly urceolate, shortly contracted into a very short neck below the very thin, nearly erect or slightly excurved rim, 8-10 mm. long, 5-8 mm. wide; valves deeply enclosed. Seeds not winged.

NORTHERN TERRITORY.—W. of Pine Creek, 13° 50′ S., 131° 46′ E., hillsides, *Eucalyptus tetrodonta*-dominant forest, 245 m., 22.x.1946, *Blake* 17282.

Type.—*Jacobs* 90 from 10 miles W. of Pine Creek (NSW, AFSC, BRI); paratype: *Jacobs* 88 from same locality (NSW, AFSC, BRI). Isotype figured in Plate 23.

Known only from the three collections cited above, all from about the same locality and in comparable habitats (map 7*C*).

The juvenile stage has not previously been described.

E. jacobsiana is easily recognized by its yellowish, more or less "stringy" bark, the very narrow, non-peltate, viscid juvenile leaves, the characteristic indumentum on the lower surface of the juvenile and intermediate leaves, the small adult leaves prominently reticulate between the primary lateral veins, the small buds and fruit, and the seeds without a terminal wing.

What is believed to be the same species was observed at Mt. Greenwood (13° 45′ S., 130° 9′ E.) during the 1946 N.A.R.S. Expedition. Herbarium material was not available, but the yellowish, stringy bark and small "bloodwood" type of leaf was noted as a peculiar combination of characters at the time, and it has not been observed in any other species. The trees occupied the crest and barren slopes of a sandstone mesa — a habitat similar to that in which the species was found later near Pine Creek.

This rather distinctive species was described from specimens collected by Jacobs "10 miles West of Pine Creek." *Jacobs* 90 was the only collection cited; it is in bud, flower, and fruit, with seeds. Blakely described the mature leaves as "alternate or occasionally opposite . . . quite glabrous but paler beneath", and the "Juvenile leaves not seen from the base of the tree, nor in the seedling stage, but only on the old fruiting branches, opposite for at least eight pairs . . . almost white beneath, with a very close somewhat velvety tomentum . . ." Jacobs (Commonw. For. Bur. Bull. No. 17, p. 60) mentioned ". . . intermediate leaves, which have a whitish undersurface . . ." then copied Blakely's English description, but immediately below stated that "*E. Jacobsiana* may be distinguished from *E. nesophila* by . . . the lanceolate leaves with a . . . whitish-tomentose undersurface"; a somewhat similar remark appears on p. 67, while on p. 35 the leaves were said to be "pubescent" on the lower surface. It is difficult to reconcile these statements from an examination of the only collection cited by Blakely. There is, however, another copious collection in fruit, *Jacobs* 88 from the same locality. Some pieces of this bear twigs with opposite leaves, which are velvety on the lower surface. One such twig with opposite leaves is present on the sheet of *Jacobs* 90 at Sydney, but not on the duplicates seen. Jacobs apparently regarded these leaves as the usual adult leaves of the species. To my mind, Blakely correctly regarded these twigs with opposite leaves pubescent beneath as reversion shoots, but the leaves are in the intermediate stage; he must have examined both collections.

Juvenile leaves and intermediate leaves form part of *Blake* 17282. The intermediate leaves are very much like those on the reversion shoots, but the stem and midrib are more setose. The juvenile leaves are much narrower, decurrent at the base (not peltate), *strikingly viscid,* and sometimes not opposite. The adult leaves are quite glabrous, even in the earliest stages of growth, and the young shoots and inflorescences are more or less viscid, though not so strongly so as the juvenile leaves.

Blakely arranged this species in his subseries *Ochrophloiae* (which includes *E. peltata* Benth., *E. torelliana* F. Muell., and others), apparently because of the yellowish cast in the bark; however, the dark timber, decurrent juvenile and other leaves, and small buds and fruits are quite at variance with his description of the group, the other members of which have pale-coloured timber, peltate leaves at least in the juvenile stages, much larger buds and fruits, and a flaky or scaly rather than stringy bark (the greater part smooth in *E. torelliana*).*

Jacobs suggested an affinity with *E. nesophila* Blakely and *E. trachypholia* F. Muell. and with *E. polycarpa*. It differs from *E. polycarpa* in the absence of a terminal wing to the seed and from all in the peculiar juvenile foliage with its characteristic indumentum, the small leaves with prominent reticulations, and the yellowish, long-fibred bark, and from one or the other in the size and shape of the buds and fruits. To judge from the material available, *E. jacobsiana* is one of the most sharply marked species in the group.

**E. peltata* sometimes has peltate leaves on adult trees. Maiden (Crit. Rev. *Eucalyptus* 5: 33, 38, 55 (1920)) presumed that the original description was based on juvenile leaves and on p. 69, in the explanation to Plate 173, Figure 2 (*E. peltata*) made the statement that "Mueller never saw mature leaves of his own species." Actually the species was described by Bentham from specimens collected by Mueller; the latter had misidentified the species as *E. melissiodora* Lindl. and had described it under this name in *J. Linn. Soc.* (*Bot.*) 3: 95 (1859). While it is usual for the adult leaves to be lanceolate and decurrent, it is worth mentioning that the excellent flowering specimens constituting *Brass* 1774 (from Newcastle Range — the type locality) taken from trees "usually 30 to 40 ft. high" have most of the leaves peltate and scabrous; and *Blake* 9983 from "tree 20-30 ft." at Homestead, in full fruit, has leaves varying from conspicuously peltate through cordate to somewhat decurrent on apparently normal adult twigs, while *Blake* 9984 from a neighbouring tree has no peltate leaves.

25. **Eucalyptus nesophila** Blakely, Key Eucalypts 90 (1934)

Juvenile leaves from narrowly lanceolate to ovate or oblong-ovate, and more or less cordate, the upper ones peltate, all petiolate and scabrous or setose. Adult leaves alternate, petiolate, narrowly lanceolate, straight or falcate, acute or acutely acuminate, tapering to a petiole of 0.9-1.5 cm., very slightly paler beneath (nearly concolorous), 10-16 cm. long, 1-2.5 cm. wide, about 6-10 times as long as wide, very faintly veined with very numerous (about 100 or more pairs of) lateral veins at an angle of 50°-60° with the midrib. Flowers in terminal corymbose panicles. Buds pyriform, rather abruptly contracted to slender pedicels 5-8 mm. long, finely and sparsely white-pustular, constricted about the middle of the calyx-tube, about 7-8 mm. long and 5 mm. wide; operculum depressed, somewhat apiculate, rather narrower than the calyx-tube and about one-quarter its length. Fruit rather narrowly ovoid-urceolate with a short neck, 1.1-1.3 cm. long and 0.7-0.75 cm. wide, about 1.5-1.7 times as long as wide, with a thin rim and 3 or 4 very deeply enclosed valves. Seeds not winged.

Type.—Hill 465 from Bathurst Island (NSW); figured in Maiden, Crit. Rev. *Eucalyptus* 5: Plate 174, Figure 7, under *E. trachyphloia* F. Muell.

Known only from Melville and Bathurst Islands (map 7*A*) and to me only from the type and *Jacobs* 34, 43. From Jacobs's account, it appears to be a tall tree with a bark very similar to that of *E. polycarpa.*

The dimensions of the fruit given above are taken from the three fruits on the types, only one of which has dehisced. Jacobs's specimens have very immature fruits, and I have seen no specimen with fruits agreeing with the dimensions given by Blakely ("15-18 × 8-12 mm."). *E. nesophila* is closely similar to *E. trachyphloia* of eastern Australia but it differs (so far as can be judged from the material available) in the larger leaves, larger fruits, and larger buds, which are more distinctly pyriform and finely and sparsely white-pustular.

26. **Eucalyptus trachyphloia** F. Muell. in J. Linn. Soc. (Bot.) 3: 90 (1859)

E. trachyphloia F. Muell. forma *fruticosa* F. M. Bail. in Qd. Agric. J. 25: 9 (1910).

Tree to 24 m. high with persistent, more or less yellowish grey, tessellately flaky, somewhat brittle bark becoming smooth on the smaller branches, and with slender, angular twigs. Juvenile leaves and intermediate leaves more or less conspicuously setose, cordate and more or less conspicuously peltate, the former opposite for a large number of pairs and oblong-lanceolate, the latter more or less oblong-ovate. Adult leaves glabrous, alternate, prominently petiolate, distinctly paler on the lower surface, lanceolate or narrowly lanceolate, more or less falcate, gradually and acutely acuminate, 7-11.5 cm. long, mostly 1-2 cm. wide, mostly 5-8 times as long as wide, with 60 pairs or more of fine lateral veins but scarcely reticulate between them. Inflorescence a terminal corymbose panicle shorter than the leaves and more or less leafy at the base. Buds finely wrinkled but neither scurfy nor scaly, obovoid and more or less pyriform, 4-5 mm. long and 3-4 mm. wide, rather abruptly contracted to very slender pedicels shorter than the calyx-tube; operculum almost patelliform, more or less apiculate. Anthers obovate-oblong, versatile, with parallel cells opening in longitudinal slits. Fruits on slender pedicels, truncate-ovoid or truncate-obpyriform with the thin rim sometimes slightly spreading, with 3 or 4 deeply enclosed valves, 7-10 mm. long, 5-6 mm. wide; seeds unwinged.

Distribution.—Queensland and northern New South Wales, in coastal and subcoastal areas (map 14*C*).

Types.—Of *E. trachyphloia*: Burnett, *Mueller* (MEL).

Of *E. trachyphloia* forma *fruticosa*: top of Glass House Mts., July 1879, *F. M. Bailey* (BRI).

27. **Eucalyptus gummifera** (Gaertn.) Hochr. in Candollea 2: 464 (1925)

Metrosideros gummifera Gaertn. Fruct. 1: 170, t. 34, fig. 1 (1788).
Eucalyptus corymbosa Sm. Spec. Bot. New Holl. 1: 43 (1793).
E. oppositifolia Desf. Tabl. Ecol. Bot. ed. 1: 222 (1804).
E. purpurascens Link var. *petiolaris* DC. Prodr. 3: 221 (1828).

Tree with brown or grey-brown, brittle, more or less tessellately flaky bark, reddish when broken, becoming smooth and grey on the smaller branches. Juvenile leaves opposite for many pairs, setose, the later ones peltate. Adult leaves alternate or sometimes subopposite, coriaceous, discolorous, lanceolate, acutely acuminate, straight or slightly falcate, 8-14 cm. long, 2-4 cm. wide, 3-5 times as long as wide, faintly veined, the intramarginal vein distinct from the slightly revolute margin and the lateral veins in 35-65 pairs at an angle of 60°-70° with the midrib; petioles 1-2.3 cm. long, flattened and relatively broad. Inflorescence a terminal corymbose panicle; pedicels slender, 7-14 mm. long. Buds smooth, turbinate-obovoid to somewhat oblong-clavate, tapering to the pedicel, about 8-10 mm. long, about 5 mm. wide; operculum not sharply demarcated from the calyx-tube, very short and more or less patelliform, thinner and more sharply circumsciss than in most other species of the *Corymbosae*. Fruits smooth and often polished before weathering, faintly ribbed, more or less distinctly urceolate, 17-20 mm. long, 11-15 mm. wide, more or less ellipsoid below the short neck, with the rather thin rim more or less recurved and sometimes strongly so; valves deeply enclosed. Seeds with acute edges, sometimes with a rudimentary wing all round but without a long terminal wing.

Distribution.—Eastern New South Wales (except in the north) and eastern Victoria (map 5*C*).

Types.—Of *Metrosideros gummifera*: fruit from specimen collected by *Banks and Solander* from Botany Bay, figured by Gaertner, loc. cit.; photograph of complete specimen (BM) reproduced by Osborn in *Proc. Linn. Soc. N.S.W.* **62**: Plate 4, Figure 1.

Of *E. corymbosa*: Port Jackson, *John White.* (not seen.)

Of *E. oppositifolia*: a seedling grown in Paris (P); figured in Maiden, Crit. Rev. *Eucalyptus* **4**: Plate 162, Figure 6.

Of *E. purpurascens* var. *petiolaris*: a seedling grown in Paris (G); portion figured by Maiden, loc. cit., **4**: Plate 162, Figure 5.

The species is distinguished by the following combination of characters: Bark rough and tessellately flaky on trunk and main branches only; some peltate juvenile leaves; adult leaves of medium width with numerous but fine and indistinct lateral veins, distinctly paler on the lower surface, and with distinctly flattened and unusually broad petioles; buds smooth with a very short and indistinct operculum, tapering to the slender pedicels; fruits more or less urceolate; and seeds without a terminal wing.

Bentham (loc. cit., 257) suggested that the species treated in this paper under the names of *E. terminalis, E. polycarpa,* and *E. dichromophloia* together with *E. citriodora* Hook. might be considered forms of *E. gummifera,* an opinion partly shared by Mueller in Eucalyptogr. dec. 5 (1880) under *E. corymbosa.* To some degree it resembles *E. polycarpa* in the bark, the strongly discolorous leaves, and the form (but not the surface) of the buds, and it resembles *E. citriodora* in the juvenile leaves, the relatively thin operculum, and the seeds without a terminal wing, but it differs from the first three in the seeds and juvenile leaves, from *E. citriodora* in the rough bark, broader leaves with fainter and more diverging veins, and smaller operculum, and from all in the rather broadly flattened petioles.

E. gummifera has commonly been known as *E. corymbosa* Sm., but there is no doubt that the correct name is the one used here. The case has been discussed by Osborn on pp. 74-5 of his paper cited above under "types".

28. **Eucalyptus intermedia** R. T. Baker in Proc. Linn. Soc. N.S.W. **25**: 674, Plate 46, Fig. 1 (1901)

E. gummifera (Gaertn.) Hochr. var. *intermedia* (R. T. Baker) Domin in Bibl. Bot. 89: 469 (1928).

Tree up to 20 m. or more high, with persistent, light grey, rather soft and brittle, more or less tessellately fissured and flaky bark up to the small branches and brown in fracture; twigs short, angular. Cotyledons reniform. Juvenile leaves opposite for numerous pairs, very shortly petiolate, oblong-lanceolate, more or less obtuse, narrowed at the base and never peltate, sparingly setose to glabrous. Intermediate leaves oblong-lanceolate, more or less obtuse, very shortly petiolate, not peltate, about the same size as the adult leaves. Adult leaves alternate, prominently petiolate (petioles 0.8-2 cm. long), somewhat shining green above, much paler and duller beneath, lanceolate, straight or somewhat falcate, acute or acutely acuminate, more or less acute at base, 8-16 cm. long and 1.5-5.3 cm. wide, 3-6 times as long as wide, rather faintly veined, with the intramarginal vein contiguous to the margin and a very large number (70-130 pairs) of lateral veins at an angle of 60°-70° with the midrib. Flowers numerous in relatively large terminal corymbose panicles; pedicels 3-8 mm. long. Buds oblong-obovoid and more or less pyriform, more or less acute, finely pustular, somewhat ribbed, 9-13 mm. long, 5-6 mm. wide; operculum conical, narrower than the calyx-tube, rather sharply demarcated from it and from half to two-thirds as long as it. Anthers versatile, oblong-obovoid with parallel cells opening in longitudinal slits. Fruit truncately obpyriform to truncately subovoid, much longer than the slender pedicels, broadest at or below the middle and rounded at the base, narrowed above into a more or less distinct neck, the narrow rim of which is sometimes slightly spreading but not recurved, from 1.1 cm. long and 1 cm. wide up to 1.8 cm. long and 1.3 cm. wide, from slightly longer than wide up to 1.5 times as long as wide. Seeds with a long terminal wing.

Distribution.—Eastern parts of Queensland and northern New South Wales (map 5*B*).

Type (lectotype).—*Bäuerlen* 314 from Ballina, N.S.W. (NSW, BRI) figured in Maiden, Crit. Rev. *Eucalyptus* 4: Plate 163, Figure 4.

E. intermedia is distinguished from the other *Corymbosae* by the following combination of characters: bark rough but rather soft, light grey, more or less tessellately flaky throughout; leaves discolorous, 3-6 times as long as wide, none of the juvenile ones peltate; buds smooth or finely pustular but not scurfy, with a relatively large operculum rather sharply demarcated from the calyx-tube, which does not taper to the base; fruits broadest at or below the middle, not recurved at the rim; and seeds with a long terminal wing.

Baker described the species from four collections from north-east New South Wales. He distinguished it from *E. gummifera* largely on differences in bark, wood, and essential oil but he also described and figured a fruit that is different from that of *E. gummifera* in not having the strongly recurved rim so characteristic of this species and so exactly figured by Gaertner. Maiden, op. cit., 4: 253 (1919), typified Baker's species on *Bäuerlen* 314 from Ballina, which he figured in his Plate 163, Figure 4, but suggested that he himself failed to understand the species. Domin treated it as a variety of *E. gummifera.*

To me, *E. intermedia* now appears to be as well-marked a species as almost any of the *Corymbosae.* I have verified the form of the fruit over a considerable range of specimens, both in the herbarium and in the field. In *E. gummifera* the bark of the smaller branches is smooth, light grey, and deciduous, while the persistent bark is distinctly reddish on fracture; in *E. intermedia* the bark is rough and persistent to the twigs, and brown on fracture. The supposed differences in the colour of the wood are not constant. But there are further differences in the buds, seeds, and leaves that seem not to have been previously observed or appreciated. The buds of *E. intermedia* are somewhat shorter and relatively broader than those of *E. gummifera,* with relatively larger, sharply delimited opercula. The difference in the seeds appears to be very sharp. Blakely described the seeds of both species as "winged", but the statement is misleading. The seeds of *E. gummifera* are somewhat turgid, with a sharp margin or very narrow incipient wing all the way round. Rather similar seeds occur in *E. maculata* Hook. and *E. citriodora* Hook., allied species with smooth, deciduous barks. On the other hand, the seeds of *E. intermedia* have a long, terminal, membranous wing (about as long as the body of the seed) like those of the allied species from Northern Australia (cf. Maiden, op. cit., 7: Plates 256 and 257).

Blakely placed *E. gummifera* in his series *Corymbosae-Peltatae* because the later juvenile leaves are distinctly peltate and *E. intermedia* was arranged in the same group probably because of its earlier association with *E. gummifera.* I have seen wild-growing plants in all stages from the cotyledonary stage onwards and have raised seedlings from *Blake* 18448 and 18450 and from other trees. Not one peltate leaf has been found on any plant of *E. intermedia,* and this is in accord with the findings of Cuthbert Hall in *Proc. Linn. Soc. N.S.W.* 39: 481-2 and Plate 38 (1914). I have not seen the source of Hall's seed, but from the opening paragraphs of his paper, it would appear that the material had been determined by R. T. Baker.

The adult leaves resemble those of *E. gummifera* in size and shape, but the lateral veins are much more numerous on the average and more distinct, and the petioles are less flattened and more slender.

It would appear that *E. intermedia* is much more closely allied to *E. polycarpa,* which it resembles in bark and seedlings and very much in habit, but it differs in having usually rather shorter twigs with shorter and broader rather darker-coloured leaves, so that the tree does not have the slightly "weeping" habit of the branchlets commonly seen in *E. polycarpa;* the buds are smoother, not scurfy, without the slight constriction about the middle of the calyx-tube, but with larger, more pointed opercula, which are rather sharply distinct from the tube; and the fruits are slightly broader in the lower half, so that they are relatively broader and more ovate in outline. The leaves of *E. polycarpa* are usually more than 5 (up to 9) times as long as wide, up to 17 cm. long.

29. **Eucalyptus zygophylla** Blakely, Key Eucalypts 88 (1934)

E. perfoliata R. Br. ex Benth. Fl. Aust. 3: 253 (1867); non Noisette ex Steud. (1821) *pro syn., nomen invalidum;* nec Desf. (1829); nec Tausch ex Maiden (1905) *pro syn., nomen invalidum;* nec A. Cunn. ex Maiden (1915); *syn. nov.*

Distribution.—Kimberley Division of Western Australia (map 14*B*).

Types.—Lectotype of *E. zygophylla*: Broome, *Fitzgerald* (NSW); figured in Maiden, Crit. Rev. *Eucalyptus* 4: Plate 158, Figures 8*b*, 8*c*, 8*d*, under *E. setosa.*

Holotype of *E. perfoliata*: *Cunningham* 238/1820 from Roe's River (K), not seen; drawing reproduced in Maiden, op. cit., 5: Plate 180, Figure 1.

The existence of Desfontaine's validly published prior homonym prevents the use of the name *E. perfoliata* R. Br. ex Benth. for this species. Although Blakely placed *E. zygophylla* in a different species, it appears to be conspecific, and this name is proposed here for the species. In the protologue Blakely cited two collections, the one cited above and one of J. B. Cleland's from the Strelley River. Both are scrappy, but since Blakely later marked Fitzgerald's sheet as "type", I have treated this as the lectotype. There are three rough labels cut from the margins of newspapers (field labels?) written up in pencil by Fitzgerald and all with the name *Eucalyptus setosa* Schau.; two of them are marked "Broome April 1905" and the other "Broome July 1906". At least two distinct collections appear to have been mixed; in the protologue Blakely mentioned that material of *E. setosa* had been associated, but this has now been removed, probably by Blakely himself.

I have seen only indifferent material of this species. The chief characters are the persistent bark and stout twigs; opposite, sessile (or also subsessile?), connate or amplexicaul leaves which are broadly ovate and obtuse to oblong or lanceolate and more or less acute, very stiff, slightly paler beneath, about 8-15 cm. long and 2.6-11.5 cm. wide, 1.2-3.6 (or more?) times as long as wide, rather faintly veined with the intramarginal vein close to but quite distinct from the edge and 20-35 (or more?) pairs of lateral veins at an angle of 50°-80° with the midrib; short, terminal, more or less corymbose inflorescence; large, sessile or subsessile flowers and fruits, the pedicels very stout when present; buds with a more or less turbinate calyx-tube about 1.5-2 cm. wide and a short or very short operculum; anthers smaller than usual for the *Corymbosae;* woody, subcylindrical to subglobose, more or less urceolate fruits 2.2-4.4 cm. long and 2.3-3 cm. wide with a very thick rim and 4 or 5 deeply enclosed valves; and seeds with a long terminal wing.

In his description of *E. zygophylla,* Blakely gave the dimensions of the fruit as "1-2 × 1.7-2.5 cm." in the Latin description and "10-27 × 17-25 mm." in the English description; the former is evidently a mistake and the latter includes the two obviously immature fruits attached to Cleland's specimen; over-mature, weathered, loose fruits in a packet with this collection are 22 mm. long and 25 mm. wide.

E. zygophylla appears to be very close to *E. abbreviata* in many ways, but the leaves of the latter have fewer (12-15) pairs of lateral veins at a more acute angle and (so far as is known) are never connate.

The differences and resemblances between the 18 species of *Corymbosae* discussed in this paper are partly summarized in the following key.

KEY TO THE CORYMBOSAE

1. Leaves with 6-15 pairs of lateral veins, 1.6-3.6 times as long as wide, rigid, sessile to very shortly petiolate, more or less cordate; younger parts usually and the older parts frequently with an indumentum of rusty or reddish to purplish scales or bristles; juvenile leaves not very different from the adult leaves; bark persistent, flaky, more or less soft and more or less brittle; fruits coarse, at least 15 mm.

long and at least 15 mm. wide, frequently sessile or subsessile; seeds with a terminal wing:

Indumentum of chiefly tiny rusty scales extending over the old leaves, which may become whitish with extreme age; leaves with 6-10 pairs of lateral veins, mostly 8-13 cm. long; petioles up to 5 mm. long; pedicels up to 4 mm. long; fruits ovate to elliptic in outline .. .. *E. ferruginea*

Indumentum of bristly hairs, sometimes confined to the twigs and inflorescence or almost or quite absent, sometimes extending to the leaves and fruit; leaves with 9-15 pairs of veins; petioles less than 3 mm. long or 0; pedicels sometimes long; fruits subglobose to strongly urceolate:

Leaves 5-10 cm. long, up to 2.2 times as long as wide, with 9-12 pairs of veins; indumentum usually well developed; pedicels 5-20 mm. long; fruits about as long as wide, the rim very rarely spreading .. .. *E. setosa*

Leaves 7-16.5 cm. long, 1.8-3.6 times as long as wide, with 12-15 pairs of veins; indumentum sparse to absent, of very short bristles; twigs usually pruinose; pedicels 0-6 mm. long; fruits distinctly longer than wide, usually smooth, with an excurving rim .. .. *E. abbreviata*

1. Leaves with 30 or more pairs of lateral veins and prominently petiolate except *E. zygophylla*, which has sessile or subsessile leaves with as few as 20 pairs of veins, sometimes markedly different from the juvenile leaves, at least three times as long as wide except in *E. latifolia*, *E. foelscheana*, and sometimes in *E. zygophylla*, *E. ptychocarpa*, and *E. porrecta;* adult plants glabrous, except that the inflorescences of *E. terminalis* and *E. polycarpa* are distinctly mealy or scurfy and the leaves of reversion shoots of *E. jacobsiana* (and perhaps of *E. dichromophloia*) may be pubescent beneath; seeds of most species with a terminal wing; bark various:

Leaves opposite and connate or cordate and sessile or nearly so, 1.3-3.6 times as long as wide with 20-35 pairs of lateral veins; fruits 22-24 × 23-30 mm., more or less urceolate .. .. *E. zygophylla*

Leaves alternate or irregularly opposite, broadly rounded to cuneate at the base, prominently petiolate, with 30-130 pairs of lateral veins:

Buds and fruits usually with very prominent vertical ridges, rarely the ridges on the fruit disappearing with extreme age; leaves markedly discolorous, sometimes more or less peltate on adult twigs, up to 35 cm. long, 2-4 times as long as wide; stamens frequently red; bark persistent, shortly fibrous, rather brittle, more or less tessellately fissured .. .. *E. ptychocarpa*

Buds and fruits smooth or finely wrinkled or scaly to scurfy but never ridged; leaves concolorous or discolorous, if the latter then not more than 20 cm. long, never peltate in the adult state; stamens (always?) cream to white; barks various:

2. Buds 4-8 mm. long, not conspicuously scurfy or scaly or pruinose except sometimes in *E. dichromophloia;* fruits 7-15, rarely up to 20 mm. long, truncate-ovoid to more or less urceolate or at least with a distinct neck, not conspicuously woody and often with frail-looking, shining sides, the orifice 4-8 mm. wide with thin or acute margins:

Fruits usually 8-15 × 8-15 mm. and about as long as or not much longer than wide, or if distinctly longer than wide then 15-20 mm. long; buds 5-7 × 3-6 mm., more or less rounded and about as wide as long; seeds with a long terminal wing; leaves not or only slightly paler beneath; bark, at least in the lower part, scaly, mottled reddish, cream, and grey, at least the smaller branches smooth and whitish, sometimes the scaly bark almost absent:

Leaves usually less than 2.5 (commonly 1.5-2 rarely up to 3) times as long as wide; fruits without a distinct neck and without a distinctly spreading rim; juvenile leaves more or less rounded, sparsely setose .. .. *E. latifolia*

Leaves 3-14 (commonly more than 3) times as long as wide; fruits with a distinct neck and a usually spreading rim; juvenile leaves more or less ovate to lanceolate, densely pubescent beneath as well as scabrous or setose .. .. *E. dichromophloia*

Fruits 7-13 × 5-8 mm., about 1.5 times as long as wide with a distinct neck and sometimes a spreading rim; buds 4-8 × 3-5 mm., pyriform or obovoid; seeds without a terminal wing (except *E. nesophila*?); leaves markedly paler beneath; bark rough, more or less fibrous, persistent to the smaller branches; juvenile leaves evidently hairy:

Leaves finely but conspicuously reticulate between the lateral veins on the lower surface, mostly 6-9 cm. long; buds 4-5 × 3 mm.; fruits 8-10 × 5-8 mm.; bark yellowish, long-fibrous, not tessellated; juvenile leaves linear, white-tomentose beneath, viscid, not peltate .. .. *E. jacobsiana*

Leaves at most faintly reticulate, 7-16 cm. long; bark grey, shortly fibrous, tessellately flaky; juvenile and intermediate leaves oblong or lanceolate to ovate, peltate, not viscid:

Buds obovoid to somewhat pyriform 4-5 × 3-4 mm.; fruits 7-10 × 5-6 mm. .. .. *E. trachyphloia*

Buds pyriform, 7-8 × 5 mm.; fruits 11-13 × 7-8 mm. .. .. *E. nesophila*

2. Buds 9-15 mm. long, in some species conspicuously scurfy or pruinose; fruits usually at least 17 and up to 40 mm. long, from about as long to 2.5 times as long as wide, in some species very woody, usually with an orifice of 9 mm. in width or more, or if smaller, then with narrow fruits and scurfy buds:

Buds nearly globular, conspicuously wrinkled, not scurfy; fruits more or less wrinkled, about as wide as long; pedicels in both flower and fruit mostly 1.2-2 cm. long, slender, and more or less angular; leaves 2-4 times as long as wide, concolorous; bark rough and tessellated throughout .. *E. porrecta*

Plants with different combinations of characters: buds not wrinkled, more or less obovoid or pyriform; leaves usually narrower or wider than in *E. porrecta*:

Leaves concolorous, more or less pallid or yellowish on both sides; fruits conspicuously woody, more or less distinctly and sometimes abruptly narrowed in the upper ½-⅓, with a thick rim: bark more or less scaly, grey and reddish, sometimes extending to the twigs and then more or less thickened towards the lower part of the trunk, sometimes confined to the base of the tree with the remainder smooth and white:

Fruits about as wide as or wider than long without a distinct neck, on pedicels up to 6 mm. long; leaves narrow; buds and flowers unknown .. .. *E. cliftoniana*

Fruits longer than wide, usually with a distinct neck; pedicels 5-17 mm. long:

Buds scurfy; leaves 3-5 times as long as wide .. .. *E. terminalis*

Buds not scurfy; leaves mostly less than twice as long as wide .. .. *E. foelscheana*

Leaves discolorous; fruits sometimes thick but not very woody, with usually a thin or acute rim; bark rough and tessellately fissured for the greater part or throughout and grey, or smooth and white nearly throughout:

Leaves 4-9, commonly at least 5 times as long as wide; fruits widest at or a little below the middle:

Buds and fruits scurfy; pedicels short (rarely as long as 12 mm.); bark tessellately flaky; juvenile leaves neither peltate nor conspicuously setose .. .. *E. polycarpa*

Buds not scurfy; pedicels 13-20 mm. long, as long as or longer than the buds, slender; buds and fruits commonly oblique on the pedicels; bark for the greater part smooth and white; juvenile leaves strongly setose, some of them peltate .. .. *E. bleeseri*

Leaves 3-6 (usually less than 5) times as long as wide; fruits widest in the lower third to about the middle; buds smooth, not scurfy; bark persistent and tessellately fissured:

Fruits more or less prominently urceolate with the rim recurved; seeds with acute margins but no long wing; buds turbinate-obovoid to oblong-clavate with a short operculum not sharply differentiated from the calyx-tube; leaves with 35-65 pairs of lateral veins; some peltate leaves on the seedlings; smaller branches with smooth bark .. .. *E. gummifera*

Fruits not urceolate, the rim not or scarcely excurved; seeds with a long terminal wing; buds oblong-obovoid and more or less pyriform, with a longer pointed operculum sharply differentiated from the calyx-tube by a slight constriction; leaves with 60-130 pairs of lateral veins; no peltate juvenile leaves, bark rough throughout .. .. *E. intermedia*

A further 14 species were recognized by Blakely as belonging to the *Corymbosae* as this group has been defined in this paper. Of these, I have seen no material of *E. haematoxylon* Maiden or *E. collina* W. V. Fitzg., and I have seen no living trees of *E. nowraensis* Maiden, *E. lamprocalyx* Blakely, *E. eximia* Schau., or *E. watsoniana* F. Muell. *E. calophylla* R. Br., *E. ficifolia* F. Muell., and *E. haematoxylon* Maiden are species endemic to south-west Western Australia with flaky bark and large, woody fruits. *E. ficifolia* is widely cultivated because of the usually brilliantly red filaments. Some supposed hybrids between this and *E. calophylla* have been described as varieties of one or other of the supposed parents; different colour forms of each also exist. *E. abergiana* F. Muell. is characterized by the discolorous leaves and large, sessile or nearly sessile, non-scurfy buds and fruits, and appears to be confined to north-east Queensland. *E. lamprocalyx* Blakely, Key Eucalypts 87 (1934) is known only from the type (*Fitzgerald* 416 from Meda, Kimberley Division, Western Australia); the specimen is without fruits, but it appears to represent a distinct species by reason of the sessile or nearly sessile but relatively narrow leaves, which are sometimes opposite; shining, purplish twigs; and shining, purplish, sessile or nearly sessile buds. By an evident error, the name *E. lamprocarpa* appeared at the head of the description, but elsewhere in the volume (pp. 17, 293, 299, 309, 323) and on the sheet the name *E. lamprocalyx* appears; the plant has nothing to do with *E. lamprocarpa* F. Muell. ex Miq. *E. collina* W. V. Fitzg. in Maiden, Crit. Rev. *Eucalyptus* 6: 419, and Plate 236, Figure 1 (1923) was based on *Fitzgerald* 844 from Bold Bluff, Kimberley Division, Western Australia, which I have not seen. If the juvenile leaves figured (Plate 236, Fig. 1*a*) really belong, then a distinct species is surely represented. But they look so much like the juvenile leaves of *E. miniata*, and the figures and descriptions of adult leaves, buds, and fruits, together with the account of the bark and twigs, so entirely agree with *E. terminalis*, that I strongly suspect that *E. collina* has been based on mixed material. It may be noted that in one place Fitzgerald stated that *E. collina* was associated with *E. miniata.*

E. peltata Benth., *E. torelliana* F. Muell., *E. eximia* Schau., *E. bloxsomei* Maiden, *E. watsoniana* F. Muell. (forming most of Blakely's subseries *Ochrophloiae*), *E. citriodora* Hook., and *E. maculata* Hook. (subser. *Maculatae*) all have unwinged seeds and some peltate leaves in the juvenile stages. The peltate-leaved stage passes very early in *E. bloxsomei* and *E. watsoniana* but is very persistent in *E. peltata* and *E. torelliana,* where peltate leaves may be found on flowering branches of tall, mature trees. *E. torelliana* has discolorous leaves at all stages and deciduous, smooth, white bark over the greater part of the tree and is associated with rain forests in north-east Queensland. The others have concolorous leaves at least in the adult stages. *E. eximia, E. peltata, E. bloxsomei,* and *E. watsoniana* have a characteristic yellowish or rusty, fibrous-flaky bark and are found in drier country; *E. eximia* is restricted to New South Wales, the others are restricted to Queensland. *E. citriodora* and *E. maculata* have deciduous, smooth, white or pink or variegated bark that is more or less deeply pitted; the former is found in Queensland from the north to about 25° S., the latter is found south from this to Victoria. *E. nowraensis* has been stated to be a hybrid between *E. maculata* and *E. gummifera* and is certainly known only from the neighbourhood of Nowra, N.S.W.

Series EXSERTAE (Benth.) Blakely

30. **Eucalyptus herbertiana** Maiden, Crit. Rev. *Eucalyptus* **6:** 429, Plate 238, Figure 2 (1923)

Small irregular tree sometimes branched from the more or less pedestal-like base, up to 9 m. high, with salmon-pink to white (or yellowish?) bark shed in pale grey, thin flakes; youngest twigs angular, soon becoming terete. Juvenile leaves opposite for a few pairs, glabrous, shortly petiolate, ovate, obtuse or emarginate, somewhat 3-nerved, on 4-angled stems, up to about 5 cm. long and 3 cm. wide; intermediate leaves rather longer and narrower. Adult leaves alternate, petiolate, dull on both sides, lanceolate or linear-lanceolate, straight or falcate, somewhat obtuse and more or less apiculate to acute, 7-23 cm. long, 1.2-2.5 cm. wide (4-12 or more times as long as wide), rather prominently veined and somewhat 3-nerved with the intramarginal vein up to 1 mm. distant from the margin, with about 27-35 or more pairs of primary lateral veins at an angle of about 35°-55° with the midrib, narrowed at the base and sometimes obliquely so to a petiole 1-1.5 cm. long. Inflorescences consisting of axillary, 3-7-flowered, simple umbels; peduncles 7-10 mm. long. Buds nearly sessile or on pedicels up to 3 mm. long, ellipsoid or somewhat obovoid, 2-3-ribbed, mostly gradually decurrent to the pedicels, about 6-8 mm. long and 4-5 mm. wide; operculum rather longer than the calyx-tube and narrower than its rim, ovoid-conical, more or less acute or apiculate.

Anthers versatile, oblong-obovate, with a large dorsal gland and parallel cells opening in longitudinal slits. Fruit on pedicels of 1-2 mm., with a cup-shaped to somewhat turbinate, more or less distinctly 1-2-ribbed calyx-tube, narrow rim, prominently exserted convex disc, and 3 or 4 deltoid-acuminate, strongly exserted, erect or spreading or slightly incurved valves up to nearly as long as the calyx-tube, in all 5-8 mm. long and 4-5.5 mm. wide.

A new record for the Northern Territory, where it is associated with *Triodia microstachya* on the Upper Pre-Cambrian quartzites and sandstones (Buldiva Quartzite). The only previously recorded collection is that of the type (map 23*A*).

The type carries buds and fruits, but lacks open flowers and juvenile leaves. *Blake* 17264 resembles the type, but has rather shorter leaves and fruits. My other collections have the larger fruits of the type, but have still shorter leaves, and the buds on No. 17217 have prominent, rather slender pedicels up to 3 mm. long; the development of pedicels is, however, a variable character.

The species resembles *E. brevifolia* in some respects, but it is readily distinguished by the longer, usually less glaucous leaves with rather prominent veins and the intramarginal vein much further from the edge, the ribbed calyx-tube, and the fruit with a taller disc and more or less subulate-acuminate valves. As to the shape and venation of the leaves, the form of the bud, and the exserted disc and valves of the fruit, *E. herbertiana* resembles species allied to *E. camaldulensis* and *E. tereticornis* Sm.

NORTHERN TERRITORY.—Near Katherine, narrow valleys among rugged sandstone hills, with *Triodia* sp., about 150 m., 19.x.1946, *Blake* 17264 (irregular, shrubby tree of 6-7.5 m., branched at or close to base with crooked, spreading or descending branches; bark throughout smooth, salmon pink, turning white with age, shed in pale grey, thin flakes; dull greyish green leaves; white filaments; buds, flowers, and fruit from same tree); same locality etc., and date, *Blake* 17265 (irregular, shrubby tree of 6-7.5 m. branched at or close to base with crooked, spreading or descending branches; bark throughout smooth salmon pink; dull greyish green leaves; buds and fruit . . . from a tree with bark just shed); Katherine Gorge, 14° 19′ S., 132° 25′ E., steep, rocky, sandstone slopes, about 120 m., 13.x.1946, *Blake* 17217 (tree of 9 m. with short trunk, oblique branches, and salmon-coloured, smooth bark throughout (recently shed); subglaucous leaves); Oenpelli, *Specht* 1103, *Specht* 1144.

Type.—Gardner 1471 from Donkin's Hill, Kimberley Division, Western Australia (NSW); figured in Maiden, loc. cit., Plate 238, Figure 2.

31. **Eucalyptus camaldulensis** Dehnh. Cat. Pl. Hort. Camald. ed. 2: 20 (1832)

E. rostrata Schlecht. in Linnaea 20: 655 (1847), non Cav. (1797).
E. longirostris F. Muell. ex Miq. in Ned. Kruidk. Arch. 4: 125 (1856).
E. longirostris F. Muell. forma *brevirostris* F. Muell. ex Miq., loc. cit.
E. rostrata Schlecht. var. *brevirostris* (F. Muell.) Maiden in Bull. Herb. Boissier (2) 2: 581 (1902).

E. rostrata Schlecht. var. *borealis* Baker & Smith, Research on the Eucalypts 75 (1902).

E. tereticornis Sm. var. *rostrata* Ewart, Handb. Forest Trees Vict. For. 301 (1925).

E. camaldulensis Dehnh. var. *brevirostris* (F. Muell.) Blakely, Key Eucalypts 135, non *E. brevirostris* Blakely, loc. cit., 183.

E. camaldulensis Dehnh. var. *obtusa* Blakely, loc. cit.

E. camaldulensis Dehnh. var. *subcinerea* Blakely, loc. cit.

E. camaldulensis Dehnh. var. *pendula* Blakely & Jacobs in Blakely, loc. cit., 135.

Tree of varied habit with smooth, deciduous, white or pale grey bark over the greater part, often with patches of darker grey, and sometimes with a variable amount of grey, flaky bark persisting on the lower part; branchlets often long and pendulous. Juvenile leaves opposite for a few pairs, petiolate, ovate to broadly lanceolate, glaucous. Intermediate leaves broadly lanceolate to lanceolate, up to about 16 × 7.5 cm., glaucous. Adult leaves dull and often pale-coloured, more or less drooping, alternate, prominently petiolate, lanceolate or narrowly lanceolate, acute or acuminate, 6-30 cm. long, 0.8-2 cm. wide, about 8-20 times as long as wide, with between 20 and 40 pairs of lateral veins at an angle of 40°-50° with the midrib, the intramarginal vein about 0.9-1.5 mm. from the margin. Inflorescences of axillary, 5-10-flowered umbels; peduncles slender, 6-15 mm. long; pedicels slender, 3-8 mm. long. Buds broadly or occasionally narrowly ovoid, rostrate, acuminate, or acute, rarely obtuse, 6-10 mm. long, 4-5 mm. wide, with a short and broad calyx-tube and a longer (up to 3 times as long), rostrate-acuminate or apiculate (rarely bluntly rounded) operculum. Anthers versatile, obovoid-oblong with parallel cells opening in longitudinal slits. Ovary prominently domed. Fruits subglobose to ovoid in outline, 5-8 mm. long, slightly narrower to slightly wider than long, with a short calyx-tube, a high domed disc, and stout, deltoid valves strongly incurved from a slightly spreading base.

NORTHERN TERRITORY.—Katherine, lower flood banks of Katherine R., about 100 m., frequent, 7.x.1946, *Blake* 17180; Kathleen Falls, Flora R., fringing forest of *Melaleuca* spp., etc., 104 m., 16.x.1946, *Blake* 17232; 13 miles NE. of Tennant Creek, in desert at least 100 yd. from creek, 24.iv.1948, *Perry* 546.

Types.—Of *E. camaldulensis*: specimen (W) from tree cultivated near Naples, Italy; photograph reproduced by Osborn in *Proc. Linn. Soc. N.S.W.* 62: Plate 4, Figure 2.

Of *E. rostrata*: not determined; presumably a specimen collected by *Behr,* near Adelaide.

Of *E. longirostris*: based nomenclaturally on *E. rostrata* Schlecht. non Cav.

Of *E. longirostris* forma *brevirostris*: Victoria, Glenelg R., *Mueller* (MEL, NSW); figured in Maiden, loc. cit., Plate 137, Figure 8.

Of *E. rostrata* var. *borealis*: Nyngan, *Bäuerlen* (NSW); figured in Maiden, loc. cit., Plate 137, Figure 3*a-d* (distinguished on chemical grounds only).

Of *E. camaldulensis* var. *obtusa*: several syntypes (NSW) of which *Cambage* 1012 from Sandy Creek, N. of Gilgunnia, N.S.W., and a specimen from the Finke R., *Kaempe*, are figured in Maiden, loc. cit., Plate 137, Figures 13 and 17.

Of *E. camaldulensis* var. *subcinerea*: two syntypes, *Cambage* 4343 from Silverton, N.S.W., and Charleville, Queensland, *Atkins* (NSW).

Of *E. camaldulensis* var. *pendula*: *Jacobs* 136, from between Birdum and Daly Waters, Northern Territory (NSW, AFSC, BRI).

Widely spread on the banks of streams and similar places over the greater part of Australia (map 16).

The prominently domed disc and prominently exserted claw-like valves of the fruit with the short calyx-tube and longer commonly beaked operculum of the bud distinguish this species from all other species in the Northern Territory. Some forms are very closely similar to *E. tereticornis* of the eastern coast and Papua, but this species is rarely glaucous, the intramarginal vein of the adult leaf is, on the whole, closer to the margin (though varying from 0.5 to 1.4 mm. from it), the pedicels are commonly shorter, the operculum is nearly always longer and narrower and often curved towards the top, and the fruits are for the most part smaller and more nearly globular in outline, with the valves incurving from the base. From our present knowledge, the two species appear to occupy distinct, though more or less contiguous, areas, but very little collecting has been done along the margins of these areas.

The variation in length of the operculum and the degree to which it is narrowed in the upper part provided the chief criteria for distinguishing most of the varieties listed in the synonymy. While some of these variations are fairly distinct in their extreme states, they appear to pass into one another by imperceptible gradations and the N.A.R.S. specimens cannot be referred to any of them. The most common form appears to be the one with an operculum abruptly constricted to a distinct beak, and this has usually been regarded as the typical form; it evidently agrees with the type of *E. rostrata* Schlecht., but the type of *E. camaldulensis* apparently had a conical-acuminate operculum.

For the interpretation of the varieties, I have relied chiefly on Blakely's descriptions, his determinations of specimens at Brisbane, and his references to published figures. The only type material I have studied is that of *E. camaldulensis* var. *pendula*.

Ewart presumably based the combination *E. tereticornis* var. *rostrata* on *E. rostrata* Schlecht., but did not definitely show this; the accompanying description would validate the name but would introduce difficulties with regard to typification, since no specimens are cited. On pp. 301 and 303 he stated that "*E. rostrata* is botanically merely a variety of *E. tereticornis* . . ." and "The variety *rostrata* can only be distinguished from *E. tereticornis* by its usually shorter operculum . . .", yet in the same paragraphs he used the name *E. rostrata* as though he considered it referred to a species distinct from *E. tereticornis.*

E. camaldulensis has usually been cited as a synonym of *E. rostrata* Schlecht. Although *E. rostrata* Schlecht. was published 35 years after *E. camaldulensis,* and is also a later homonym of *E. rostrata* Cav., Schlechtendahl's name continued in general use until 1934 when Blakely took up Dehnhardt's name for the species. *E. camaldulensis* was based on a tree, 40 ft. in height, cultivated in the Hortus Camaldulensis near Naples, Italy, and a specimen was sent by Dehnhardt to Vienna where it was seen by Maiden in 1902 and by Osborn in 1936, and the latter published a photograph of it in the paper cited above. Fruits were described in the protologue but the specimen has buds only. Neither Maiden nor Osborn appear to have any doubts concerning the identification of Dehnhardt's specimen with *E. rostrata* Schlecht. although Osborn did remark that "the operculum is conical rather than rostrate". However, it would be interesting to learn the history of a tree of this species which could attain the height of 40 ft. in Italy by 1832.

Series SUBEXSERTAE (Benth.) Blakely

32. **Eucalyptus brevifolia** F. Muell. in J. Linn. Soc. (Bot.) 3: 84 (1859)

E. pallidifolia F. Muell. Fragm. 3: 131 (1863).

An irregular, often shrubby tree up to 9 m. high but usually much less, with smooth, pure white to pale grey bark shedding in flakes, or turning pinkish immediately before it sheds; branches and twigs brittle, the latter slender. Intermediate leaves suborbicular or broadly ovate, very glaucous, up to about 8 cm. long and nearly as wide. Adult leaves alternate, petiolate, dull and more or less glaucous, lanceolate to narrowly oblong or linear, more or less obtuse to more or less acute or acuminate, usually 4-8 cm. long and 1-2 cm. wide, usually 3-6 times as long as wide, thick, with very indistinct veins; primary lateral veins in about 20 pairs, and making an angle of 30°-50° with the midrib. Inflorescences of axillary, pedunculate, 4-6-flowered umbels. Buds subsessile to very shortly pedicellate (pedicels up to 2 mm. long), broadly ellipsoid to nearly globular, from 5 mm. long and 4 mm. wide up to 8 mm. long and 6 mm. wide; operculum slightly shorter than the calyx-tube, hemispherical to somewhat conical. Anthers versatile, obovate-oblong, with parallel cells opening in longitudinal slits and a dorsal gland. Fruits subsessile to very shortly pedicellate, with a cup-shaped or truncate-ovoid calyx-tube, narrow rim, convex or concave disc up to 1.5 mm. thick, and short to relatively long, erect or insloping, exserted valves, in all from 5 mm. long and wide up to 7 mm. long and 6 mm. wide.

NORTHERN TERRITORY.—Fifteen miles NW. of Limbunya Station, on skeletal soils on dolerite, 30.vi.1949, *Perry* 2311; 29 miles WSW. of Victoria River Downs, steep, rocky slopes with *Plectrachne* and *Triodia*, 18.vi.1949, *Perry* 2170; 20 miles NW. of Wave Hill Police Station, on lateritic, yellow podsol on sandstone, 27.vi.1949, *Perry*

2261; near Powell Creek, dominant in *Eucalyptus-Triodia* scrub, reddish soil, 2.xi.1946, *Blake* 17360; 6 miles N. of Helen Springs, 29.vi.1947, *Perry* 135; 16° 8′-10′ S., 134° 37′-43′ E., forming large communities on laterite slopes and tablelands, 166-204 m., 3.v.1947, *Blake* 17614; 20.2 miles N. of Tennant Creek, 30.vi.1947, *Perry* 160; 8 miles N. of Tennant Creek, stony rise, 24.iv.1948, *Perry* 545; 7.9 miles N. of Tennant Creek, 30.vi.1947, *Perry* 155; 8 miles NW. of Tennant Creek, stony, truncated, lateritic soil with *Triodia*, 25.iv.1948, *Perry* 575; 8 miles NE. of Tennant Creek, shallow, stony soil on flat with sandstones and quartzites, 24.iv.1948, *Perry* 555.

Lectotypes.—Of *E. brevifolia*: Victoria R., May 1856, *F. Mueller* (K, MEL, BRI).

Of *E. pallidifolia*: Upper Victoria R., *F. Mueller* (MEL, NSW, K, BRI); figured in Maiden, Crit. Rev. *Eucalyptus* 3: Plate 93, Figure 11.

This species is widely spread in the Northern Territory and north-west Queensland, chiefly in the area between the 12-in. and 25-in. isohyets (map 21). It is especially characteristic of the rugged hills of the steeply dipping earlier Pre-Cambrian schists etc., but is also found on the later Pre-Cambrian sandstones and quartzites and rarely on other rocks; species of *Triodia* or sometimes *Plectrachne* are generally associated.

E. brevifolia is usually easily recognized by its irregular, often shrubby habit with smooth, white or pale grey bark (Plate 6, Fig. 3), its small, narrow, dull adult leaves with very obscure veins contrasting rather sharply with the very broad and very glaucous intermediate leaves. The immature fruits sometimes strongly resemble those of *E. microtheca*, and this was partly responsible for the confusion with this species discussed below; at maturity the resemblance is not so close, and in any case the axillary, simple umbels readily distinguish it from *E. microtheca* with its terminal and subterminal panicles, while the two species are quite distinct in habit and habitat. The fruits of *E. brevifolia* vary somewhat in size, width of disc, and degree of exsertion of the valves. On the specimens from the neighbourhood of the Victoria River, the fruits are 6-7 mm. long and 5-6 mm. wide with a relatively broad disc and short valves; *Blake* 17360 at the other extreme, has fruits only 5 mm. long and broad, with a relatively much thinner, more or less descending disc and larger valves; most of the 30 collections seen appear to be more or less intermediate, though ripe fruit is not represented on most of these.

The earliest juvenile leaves I have seen are those forming part of *Blake* 17614 cited above; there is only one pair of opposite leaves, which are broadly ovate, prominently petiolate, and subglaucous. Blakely (op. cit. 137) described "3-4 or more pairs" of broad, pale green juvenile leaves. Maiden, op. cit., 8: 295, described seedlings having 4 pairs of lanceolate leaves.

E. brevifolia was described by Mueller as a shrub or small tree with smooth, whitish grey bark, fulvous branchlets, few-flowered axillary umbels, etc., "in eremis terrae tabularis ad flumina Victoria et Sturt's Creek, in plaga Arnheim's Land et circum sinum Carpentaria" (in desert places of the tableland at the Victoria River and Sturt's Creek, in the region of Arnheim's Land and around the Gulf of Carpentaria). Bentham (Fl. Aust. 3: 223 (1867)) cited it along with *E. microtheca* F. Muell. as a synonym of *E. brachypoda* Turcz. Criticizing Bentham's opinion in Fragm. 11: 14 (1878), Mueller stated he thought that *E. brevifolia* was distinct from *E. microtheca* on bark characters, but that a fresh inquiry was necessary. Later, in Eucalyptogr., dec. 10 (1884), he treated it as a synonym of *E. microtheca* under which he also wrote "In the variety brevifolia the leaves become reduced to $\frac{1}{4}$ inch width and the fruits to 1/6 or even 1/8 inch". Maiden, op. cit., 2: 51 (1910) accepted *E. brevifolia* as a synonym of *E. microtheca* with the curious remark "It is the older name and would have replaced *E. microtheca* had not there been an earlier *E. brevifolia*". Actually, *E. brevifolia* F. Muell. and *E. microtheca* F. Muell. were published simultaneously (in the same paper), and I can find no reference to an earlier *E. brevifolia.*

The characters given above do not well accord with the characters given for *E. microtheca* in the same paper. During the search for a smooth-barked species to which the description might apply, *E. pallidifolia* F. Muell. Fragm. 3: 131 (1863) suggested itself. The description of this and the habitat "In tractu arenoso-rupestri (sandstone table-land) Australiae boreali-occidentalis satis frequens; e.g. ad flumen Victoriae et rivum Sturt's Creek" (rather frequent on the sandstone tableland of north-west Australia; e.g., at the Victoria River and Sturt's Creek) accord very well, and it would be surprising if Mueller had omitted such a distinctive and widely spread species from his paper of 1859.

A search through the specimens of *E. pallidifolia, E. microtheca,* and other less likely species in the Melbourne Herbarium failed to reveal any specimen labelled *E. brevifolia* by Mueller. The suspicion arose that possibly Mueller had omitted to label the specimens he kept after sending some to Hooker, and forgetting his *E. brevifolia,* later used the same specimens to draw up his description of *E. pallidifolia.*

Through the courtesy of the Director, Royal Botanic Gardens, Kew, and Mr. V. S. Summerhayes, I have received photographs and fragments of all the (four) sheets at Kew labelled *E. pallidifolia* or *E. brevifolia.* All bear a printed slip reading: FLORA AUSTRALIENSIS./named by Mr. BENTHAM./ Two of these sheets are evidently part of the same gathering (Upper Victoria River, Sandstone tableland) which is also represented at Melbourne. Another collection from "Stony ridges, Victoria River, May 1856" is represented in both herbaria. The labels were originally written up by Mueller as simply "Eucalyptus . . ." and they were received like this at Kew. Later, Mueller wrote in "pallidifolia" on his labels in Melbourne. The Kew sheets have been labelled firstly as *E. brevifolia* and at a later date as *E. pallidifolia;* the later determination is in Bentham's writing, with a reference to the volume and page of the Flora Australiensis; the earlier writing (in pencil?) also appears to be Bentham's. The fourth Kew sheet has specimens from two collections mounted on it. To the left is a fruiting specimen of *E. microtheca* under which is a narrow label bearing the words "Eucalyptus brevifolia F. Muell/ Cooper's Creek Howitt's Exped."/. What appears to be "E. microtheca F.M." has been written on the sheet against the label, but the writing is very faint and has not photographed very well. Close to the top, on the label itself, Bentham has written "E. brachypoda Turcz.", and this determination apparently applies to the whole sheet. On the right of the sheet are two pieces of the species under discussion. The label beneath them bears the following in Mueller's writing: Eucalyptus brevifolia/ferd Mueller/Gulf of Carpen/taria/ferd. Mueller/; above the label, on the sheet, Bentham (?) has written "E. brachypoda". The specimen is in slightly immature fruit and is the only one seen that has been labelled *Eucalyptus brevifolia* by Mueller. It is not represented in Melbourne. It could be taken as the type except for the following considerations:

(1) The fruits, though slightly immature, are much smaller than those on the other specimens, and correspond with the smaller fruits mentioned by Mueller after the original description of both *E. brevifolia* and *E. pallidifolia.*

(2) There must have been some evidence available at the time for Bentham (?) to have labelled the other sheets *E. brevifolia.*

(3) The collection from "Stony ridges, Victoria River, May 1856" agrees well with the original description, including the note on bark on the Kew sheet.

For these reasons, it is suggested that Mueller's collection from "Stony ridges, Victoria River, May 1856" be taken as the lectotype. Maiden has figured a specimen from the upper Victoria River (op. cit. 3: Plate 93, Fig. 11 (1914)), apparently one from "Sandstone tableland" (cf. p. 29), and on p. 43, in the explanation to the plates, states that it is the type of *E. pallidifolia;* this may be taken as a deliberate act of typification. In any case there is no doubt that *E. brevifolia* and *E. pallidifolia* were founded on specimens from the same series of collections, and that they refer to the same species. The correct name for the species is accordingly *Eucalyptus brevifolia* F. Muell. The confusion with *E. microtheca* seems to have originated from the association of the specimens from the Gulf of Carpentaria and from Cooper's Creek.

E. brachypoda Turcz., to which Bentham referred *E. brevifolia* and *E. microtheca,* has been shown by F. Mueller (Fragm. **11:** 14 (1878)) to be conspecific with *E. rudis* Endl. *E. rudis* is closely similar to *E. camaldulensis* and appears to be confined to south-western Western Australia.

33. **Eucalyptus alba** Reinw. ex Bl. Bijd. Fl. Ned. Indië 1101 (1826)

E. leucadendron Reinw. ex de Vriese, Pl. Ind. Bat. Or. 63 (1856); non A. Cunn. ex Maiden (1904).

E. platyphylla F. Muell., J. Linn. Soc. (Bot.) **3:** 93 (1859).

E. alba Reinw. var. *australasica* Blakely & Jacobs in Blakely, Key Eucalypts 137 (1934).

E. platyphylla F. Muell. var. *tintinnans* Blakely & Jacobs in Blakely, Key Eucalypts 138 (1934).

Tree up to 18 m. high, sometimes small and somewhat shrubby, with smooth, deciduous, white to salmon-pink bark and more or less deciduous leaves. Juvenile leaves ovate or broadly elliptical, broadly rounded at the tip and narrowed to broadly rounded at the base, with about 6 pairs of primary lateral nerves, shortly petiolate, opposite for 3-5 pairs; intermediate leaves alternate, ovate or more or less deltoid, up to 30 cm. long and nearly as wide. Adult leaves alternate or sometimes more or less opposite, concolorous and usually dull, on petioles 1.5-5 cm. long, variable in shape from deltoid or rhomboid-ovate to lanceolate and obtuse or acute to acuminate, about 6-18 cm. long, mostly 1.5-9.5 cm. wide, usually 1.3-7 times as long as wide but sometimes wider or narrower, with 10-15 pairs of primary lateral veins at an angle of 30°-60° with the midrib, the narrower leaves with the more numerous and steeper veins. Inflorescences of axillary or shortly supra-axillary, pedunculate, several-flowered umbels, sometimes associated with the axils of fallen leaves; bracts evident on very young inflorescences; pedicels 0.5-8.5 mm. long, more or less strongly compressed, 1-3 mm. thick. Buds broadly obovoid or subglobular to fusiform and then more or less acuminate, 4.5-11 mm. long, 3.5-7 mm. wide; operculum from somewhat shorter to somewhat longer than the calyx-tube, hemispherical to more or less conoid, muticous to distinctly umbonate or mucronate. Anthers obovate-oblong, versatile, with a large dorsal gland and parallel cells opening in longitudinal slits. Fruit more or less hemispherical, abruptly narrowed to somewhat attenuated to the pedicels, with a narrow, rounded rim rarely more than 1 mm. thick, and 3 or 4 valves from nearly flush with the rim to distinctly but shortly exserted, in all 4-9 mm. long and 5-9 mm. wide; disc obscure, lining the calyx-tube.

NORTHERN TERRITORY.—12° 49′-50′ S., 130° 43′-47′ E. (near Bynoe Harbour), forming open parkland on drainage flat, 30 m., 13.viii.1946, *Blake* 16797; Coolibah Swamp, 13° 3½′ S., 131° 26′ E., slope and crest of low ridge in "orchard country" dominated by *E. clavigera* and *E. foelscheana*, about 40 m., 28.ix.1946, *Blake* 17083; 7 miles S. of Pine Creek, on granite slopes, 29.viii.1948, *Perry* 1945; near Brocks Creek, in *Eucalyptus* forest on stony hills, about 145 m., 25.vi.1946, *Blake* 16125; 18 miles SW. of Katherine, 3.vi.1949, *Perry* 1983.

The following collection appears to represent a hybrid between *E. alba* and *E. tectifica*:

About SW. of Katherine, near King R., sandstone tableland, lateritic sandy soil, mixed *Eucalyptus* forest, about 120 m., 18.x.1946, *Blake* 17260 (tree, 6-7.5 m. high with smooth salmon-coloured bark; pale yellowish green leaves).

Types.—Of *E. alba*: *Reinwardt* 1342 from Timor (L).

Of *E. leucadendron*: based on same specimen as *E. alba;* figured by de Vriese (loc. cit., Plate 5), the figure reproduced in Maiden, Crit. Rev. *Eucalyptus* 3: Plate 105, Figure 1.

Of *E. platyphylla*: "Fertile plains of the Upper Burdekin," *F. Mueller* (MEL); Plate 27 and Plate 30, Figure 10.

Of *E. alba* var. *australasica*: *Jacobs* 48 from 22 miles S. of Darwin (NSW, AFSC, BRI); Plate 25, Figure 1 and Plate 30, Figure 1. *Paratype.*—Jacobs 46 from Bathurst Island (NSW, AFSC, BRI); Plates 25, Figures 2 and 3; and 30, Figure 2.

Of *E. platyphylla* var. *tintinnans* (lectotype): *Jacobs* 77 from Wandi (NSW, AFSC, BRI); Plate 28 and Plate 30, Figure 6.

Widely spread over northern and north-eastern Australia, extending northwards to Timor, Flores, Solor, and southern New Guinea (map 19). While commonly found on flat or nearly flat ground, it extends up the hill-slopes and in some places it is more or less restricted to the ridges.

From other species with prominently petiolate leaves, axillary, simple umbels, and versatile anthers opening in longitudinal slits, it is best distinguished by the prominent venation and the thin rim and obscure disc of the fruit.

E. alba and *E. leucadendron* were based on the same specimens from Timor. The tree was characterized by the smooth, white bark, somewhat deltoid-ovate or ovate-lanceolate acuminate leaves obtuse or acute at the tip, and long-pedicelled buds with a conical and somewhat acute operculum; the figure cited above shows a distinctly apiculate operculum. The type, in bud and flower, carries leaves 2.7-3.5 times as long as wide, pedicels 4-8 mm. long, and buds 7-8 mm. long and 5 mm. wide; the operculum is shortly apiculate-acuminate with the point about 0.7 mm. long. About 25 collections have been seen from the Lesser Sunda Is. and they vary considerably between one another (Plate 24, Figs. 1-3; Plate 30, Figs. 15 and 17; these plates were prepared before most of the Malaysian specimens, including the type, were seen).

E. alba var. *australasica* was founded on *Jacobs* 12, *Jacobs* 46, and *Jacobs* 48, all from the neighbourhood of Darwin. *Jacobs* 48 is marked TYPE at Sydney; I did not study the fruit on this sheet in detail, and there is none on the sheet at Brisbane. The form was characterized by lanceolate adult leaves, shortly pedicellate, broadly ovoid to subglobular, obtuse or subacute buds 5 mm. long and 4 mm. wide, and small, more or less turbinate fruits 4 mm. long and 5 mm. wide. *Holtze* 1253 from Darwin (MEL) and part of *Blake* 16797 are the only other specimens that at all closely match Jacobs's material. *Blake* 16797 consists of many sheets from two trees; the leaves from each tree are quite variable (as they are on *Jacobs* 46), from ovate and more or less obtuse to narrowly lanceolate and acute to acuminate (Plate 26). One of these trees was tall and erect, about 18 m. high, and the specimens were obtained from a branch from about the middle of the crown, shot down by the other members of the party; because of its height, any possible effects of fire on the leaves can be excluded. The buds from this tree are noticeably larger than the others, about 7 mm. long and 5-6 mm. wide, and some of them are slightly apiculate; these larger apiculate buds resemble those on the specimens from Timor and Solor more closely than they do those on Jacobs's specimens. *Specht* 1216 from Oenpelli resembles Jacobs's specimens in facies, but the buds and fruits are larger on much shorter and thicker pedicels or subsessile (Plate 30, Fig. 9).

E. platyphylla was characterized by the ovate- or cordate-orbicular to somewhat rhomboid or rarely ovate-lanceolate leaves, short or very short (and thick) pedicels, and blunt broad buds. The type is very scrappy, but has a few leaves, two buds, a few open flowers and some developing fruits (Plate 27 and Plate 30, Fig. 10); apparently ripe fruit was described in the protologue, but none is now associated with the specimen. The buds are about 5 mm. long and wide with a rounded operculum, but they appear to be not quite mature since the calyx-tube of the open flowers is 6 mm. wide. The pedicels are up to 3 mm. long, but some of the developing fruits are quite sessile. The field label reads: Eucalyptus platy-/phylla ferd Mll/Fertile plains of/the Upper Burde-/kin DM/. Although this specimen appears not to have been studied since Bentham's day, the name has generally been applied to all forms growing in Queensland and sometimes to those growing in New Guinea. There is, however, considerable minor variation found in this area. Narrow leaves are sometimes found such as those on Shearer's specimen figured by Maiden (op. cit. 3: Plate 106, Fig. 3*b*) and they may be long-acuminate as in *Court* 87. The pedicels vary in length as described for the type, but they are usually stout. Buds vary in length from 6 to 8 mm. and in breadth from 5 to 7 mm.; the operculum may be obtusely rounded or subacute or distinctly apiculate (Plate 30, Figs. 10-12). When the buds are both evidently pedicellate and apiculate (e.g. Bancroft's specimen from Palm Island figured in Plate 30, Fig. 12) they closely resemble those of some of the specimens from Timor. The fruits (cf. Plate 30, Fig. 13) vary in size from 5 mm. long and 7 mm. wide up to 7 mm. long and 8.5 mm. wide. The specimens from New Guinea mostly resemble those from Queensland, though *White* 210 has fruits and pedicels like those of *Teysmann* 7946 from Timor, and *Brass* 771 is scarcely different (Plate 30, Fig. 16).

The name *Eucalyptus platyphylla* var. *tintinnans* was applied to more or less scrubby trees from hilly country to the south-east of Darwin with salmon-coloured bark, more or less deltoid leaves, and small, pedicellate buds and fruits. Although there is no doubt as to the form or forms to which the name was applied by the authors, the actual typification of this name is a problem. In the protologue, *Jensen* 376 and 404 were cited, together with a generalized statement by Jacobs concerning chiefly distribution and habit, but without mention of particular collections. In the Sydney Herbarium *Jacobs* 89 is marked TYPE and *Jacobs* 98, *Jensen* 404 and *Jensen* 427 are all marked CO-TYPE. On his map Jacobs has marked a spot south-east of Pine Creek as the type locality; this could refer more or less to *Jacobs* 77 and *Jensen* 404, but since there is a cluster of numbers about Pine Creek, this should not be taken too critically. In the original description, the buds are described as globose to elliptical and 4-5 × 4-5 mm., and the fruits 4 × 5 mm. But *Jacobs* 89 has buds 6 × 5 mm. (Plate 30, Fig. 7) and no fruits; *Jensen* 404 has relatively long and narrow buds about 6 × 4.5 mm. (Plate 30, Fig. 5) and no fruits; *Jensen* 427 (from Burrundie, in bud and flower) has buds 5-6 × 4-5 mm., but they are evidently immature; and *Jacobs* 98 corresponds to *E. apodophylla* var. *brachyphylla* (see below). But there is one collection with buds 5 × 5 mm. and old fruits 4 × 5 mm.; this is *Jacobs* 77 from Wandi, and since it agrees best with the original description, it is selected as the lectotype, although it was not explicitly cited in the protologue (Plate 28 and Plate 30, Fig. 6; the fruits were too damaged for photographing).

Some of the leaves from these specimens are indistinguishable from those on some of the specimens from Timor and most of those from Queensland; others appear to be more loosely veined because of the weaker development of the secondary lateral veins, but this weaker development is also found in leaves from Queensland specimens. The pedicels vary from 1 to 5 mm. in length, and the operculum may be rounded, subacute or apiculate as in other forms. Except for the smaller size of the buds, *Jensen* 404 closely resembles *Teysmann* 7951 (cf. Plate 30, Figs. 5 and 17); part of *Jacobs* 89 and Bancroft's specimen from Palm Island are scarcely different (Plate 30, Figs. 7 and 12), while *Jacobs* 92 differs only slightly in the relatively broader buds and the irregular development of secondary lateral veins in the leaf. Fruits are known from few collections only; they are similar in shape to those from Timor, but smaller, from 4 × 5 mm. up to 5 × 6.5 mm.

Although these four forms appear to be rather distinctive when type material only is studied, it appears to be quite impossible to distinguish them when a larger suite of specimens is available (cf. Plates 24-29 and 30, Figs. 1-18). There is so little correlation between the differences in foliage, pedicels, buds, and fruits, and there are so many apparent intermediates, that it is no easy matter to find two specimens that match exactly among the 120 or more collections I have referred to *E. alba*. Some suggestion of this lack of correlation has already been made. Other collections worthy of mention are *Jacobs* 42 from Bathurst Island with fruits and pedicels quite like those of *Teysmann* 7951 and leaves more like those of some Queensland plants (cf. Plates 24, 27, and 30, Figs. 17-18); *Specht* 575*a* from Groote Eylandt with fruits and some of the leaves like those from Timor and Solor but with subacute, shortly and broadly pedicellate buds more like those on some specimens from Queensland such as Plant's collection from Charters Towers (compare Plate 29 and Plate 30, Fig. 8 with Plate 24, Fig. 1 and Plate 30, Figs. 11, 15, 17); *Specht* 575*b* from a neighbouring tree with all leaves broadly ovate and acute, not well matched by any of the described forms; and *Specht* 341, also from Groote Eylandt, with unusually large and prominently cordate leaves, but with subsessile fruits about 7-8 mm. long and 9 mm. wide.

It is also evident that there is no correlation between differences in morphological characters and geographical distribution. So far as my experience in the field permits an expression of opinion—and I have seen trees growing naturally over the greater part of the known range of the species in Australia—there seems very poor correlation between observed differences in bark and habit and other characters. *E. alba* var. *australasica* and *E. platyphylla* resemble each other in bark and general form and correspond well with Reinwardt's description of the trees in Timor. *E. platyphylla* var. *tintinnans* appears the most distinctive form because of the salmon-coloured bark, its scrubby habit, and its occurrence on stony hills; however, the bark of this form may be cream according to Jacobs's statement in the protologue and it may turn pale grey at least when being shed (*Blake* 16125), while larger trees were observed in 1946 (*Blake* 17083), and trees in Queensland sometimes occur on stony hillsides, are sometimes scrubby in appearance, and sometimes have buff or reddish bark for short periods at least (*White* 10131, *Blake* 18507, 18652, *L. S. Smith* 4353). It should, however, be pointed out that all observations on trees in the Northern Territory have been made during the dry season, chiefly from June to October, and there is no evidence that the bark is shed simultaneously throughout the area.

An extensive study of the juvenile leaves may provide important data, but, to judge from the available material, there is no appreciable difference between the juvenile leaves of *E. platyphylla*, *E. platyphylla* var. *tintinnans*, and *E. alba* var. *australasica*. According to Maiden's account (op.cit., 8: 300-4) there appear to be slight differences between young seedlings grown at Sydney from seed from Queensland and Java (Timor ?), but the account is insufficient for a general comparison, and there appears to be some inconsistency between the statements on pp. 302 and 304.

The consideration of all these facts led me irresistibly—although very unwillingly at first—to the opinion that all these forms are conspecific. The range of variation is considerable, but no greater than in many other species, and at least in some cases appears to be as great between neighbouring trees as between trees from distant localities (cf. *Blake* 16797, *Specht* 575*a* and 575*b*, *Jensen* 404 and *Teysmann* 7951, and *Jacobs* 89 and *Bancroft*). Certain trends in the variation of some organs also reduce the importance to be attached to such variation. It has been observed that the number of lateral veins increases as the ratio of length to breadth of the leaf increases, and at the same time the angle these veins make with the midrib becomes more regular and more acute. The length of the petiole varies according to the absolute width of the leaf, with the ratio of length of petiole to width of leaf remaining fairly constant. The point on the operculum is the most conspicuously variable character of the bud; if this point be regarded as an appendage which may be well developed, rudimentary, or absent and which may be neglected in comparisons, then the variation in the shape of the bud is quite small and correlated with slight differences in relative breadth. There is little essential difference in the shape of the fruit, but if the pedicels are both short and stout, the fruit sometimes tends to be somewhat turbinate; in other words, fruits and pedicels are less sharply differentiated if the latter are short or stout, particularly if the former are also small (generally speaking, the shorter the pedicel, the stouter it appears).

E. platyphylla, E. bigalerita F. Muell., and *E. pastoralis* S. Moore were at first treated as conspecific with *E. alba* by Maiden (op. cit., **3**: 90-7 (1914)). Later (op. cit., **8**: 98-102 (1929)), he treated *E. alba, E. platyphylla,* and *E. pastoralis* as distinct species and referred *E. bigalerita* to *E. platyphylla* in accord with his statement on p. 98 that his Plate 107, Figure 6 was drawn from the type of *E. bigalerita;* in the explanation to this plate it was stated that this figure was drawn from a Fitzgerald specimen from the Calder River (= *Fitzgerald* 1445) collected 46 years after the name was published. From an examination of Mueller's type, it is evident that *E. bigalerita* and *E. pastoralis* are conspecific; they are discussed below under the former name.

Maiden also (op. cit., **3**: 92-3) referred *E. populifolia* Hook. in Mitch. J. Exped. Trop. Austr. 204 (1848) to *E. alba,* and stated it was not the same species that Hooker described and figured under the same name in Hook. Ic. Pl. t. 879 (1852); Mitchell's specimen, collected near Mt. Owen, came from an area far removed from the known range of *E. alba* and must represent the same species as described and figured in 1852. Because of the earlier homonym of Desfontaines, *E. populifolia* Hook. should be called *E. populnea* F. Muell., as was pointed out by Cameron in Vict. Nat. **63**: 42 (1946).

E. tectifica F. Muell. was referred to *E. alba* by Bentham (loc. cit., 243); this name belongs to a distinct species discussed later on in this paper.

E. decaisneana Bl. in Mus. Bot. Lugd.-Bat. **1**: 83 (1849) was treated as a synonym of *E. alba* by Maiden (Crit. Rev. *Eucalyptus* **3**: 92-3 (1915).) and Blakely (Key Eucalypts 516 (1934)). Blume based his name on a specimen at Leiden received from Paris labelled: Eucalyptus obliqua L'herit. / Timor. This specimen is evidently part of the material on which Decaisne based his report of *E. obliqua* from Timor in Nouv. Ann. Mus. d'Hist. Nat. 2: 454 (1834) and this reference was quoted by Blume. The Leiden specimen is in flower, with an operculum in a packet, and certainly belongs to *E. obliqua* L'Hérit., a species of New South Wales, Victoria, Tasmania, and South Australia. There seems no doubt that the specimen had been wrongly labelled as to locality, and the name *E. decaisneana* must be treated as a synonym of *E. obliqua;* it has sometimes been misapplied to a second species of the Lesser Sunda Islands to be discussed elsewhere, of which fruits have been mistakenly figured in Plate 30, Figure 14, as *E. alba.*

E. moluccana Roxb. Fl. Ind. 2: 498 (1832) was also treated as a synonym of *E. alba* by Maiden (loc. cit.), but I cannot reconcile this with

Roxburgh's description and the notes on the type (BM, marked as coming from Amboina) supplied by Dr. R. Melville.

Two possible hybrids have been noted. One of these has been described as *E. apodophylla* Blakely & Jacobs var. *brachyphylla* Blakely & Jacobs, though Jacobs strongly suspected its hybrid nature, as shown by his herbarium labels and his discussion with me in 1947. The form, represented by *Jensen* 375 from Wandi (type) and *Jacobs* 98 from Pine Creek flats, approaches *E. apodophylla* in leaf shape, but has distinct petioles; the fruits and buds are more like those of *E. alba* (although these species may closely resemble one another in these characters) and the plants appear to be hybrids between the two species.

Blake 17260 was collected from a tree about SW. of Katherine, near the King R., associated with *E. alba* and *E. tectifica*, and it appears to represent a hybrid between these species. In general appearance, the tree resembled one of *E. alba* (*E. platyphylla* var. *tintinnans*) with elongated leaves; the fruits are narrower, approaching in shape those of *E. tectifica*, while the buds and coppice leaves also resemble those of this species; the axillary umbels and the anthers, however, resemble those of *E. alba* and its allies.

34. **Eucalyptus bigalerita** F. Muell. in J. Linn. Soc. (Bot.) 3: 96 (1859)

E. pastoralis S. Moore in J. Bot. 40: 27 (1902).

E. bigalerita is fairly easily recognized in the field by reason of its smooth, salmon-coloured to whitish bark and its heavy-looking crown of large, more or less deltoid, long-petiolate, and more or less pendulous, thick, shining, green leaves and large, shining, green intermediate leaves, but in technical characters it is very close to *E. alba*, from which it differs in having the leaves thicker with fainter veins, fairly regular in shape, and on the average larger with longer petioles, in having larger buds and thicker-walled, usually larger fruits (compare Fig. 19 with Figs. 1-18 on Plate 30). The leaves are fairly constantly deltoid to rhomboid-ovate, often somewhat cordate, mostly from 7.5 × 6.5 cm. up to 14 × 12 cm., mostly from slightly longer than wide up to 1½ times as long as wide, on petioles 3-5.5 cm. long; there is commonly a second intramarginal vein some distance in from the edge; as in the broader leaves of *E. alba*, there are about 10-12 pairs of lateral veins, mostly at an angle of 30°-45° with the midrib. The peduncles are stout or very stout; the pedicels also are stout, 3-4 mm. thick, commonly less than 3 mm. long and sometimes rudimentary but sometimes up to 4 mm. long. The buds are subglobular, passing gradually into their pedicels, about 11-12 mm. long and 10 mm. wide, with the hemispherical operculum about as long as the calyx-tube. The fruits are more or less turbinate to cup-shaped with rather thick walls and disc (together 1-1.5 mm. wide at the orifice) and slightly exserted valves, in all 7-9 mm. long and 9-11 mm. wide.

WESTERN AUSTRALIA.—Twenty-five miles E. of Carlton Station, alluvial, deep, sandy lateritic yellow podsol, 29.vii.1949, *Perry* 2656. NORTHERN TERRITORY.—Near

Ryan's Creek, 13° 11½′ S., 131° 23′ E., creek and river flats, 29 m., 8.vii.1946, *Blake* 16391; about SSE. of mouth of Daly R., 13° 51′-53′ S., 130° 20′-30′ E., alluvial flats of Hermit Ck., 23 m., 25.vii.1946, *Blake* 16624; 40 miles SW. of Katherine, edge of shallow depression in limestone soil, 3.vi.1949, *Perry* 1998; 4.1 miles E. of "Dunmarra", 15.vii.1947, *Perry* 379.

Types.—Of *E. bigalerita*: W. of Mataranka, near junction of King R., Dry R., and Darrinyan Ck., *F. Mueller* (MEL); the label reads "Fertile plains on the head of the Roper 3-5 July 56", and at this date Mueller was in the locality cited above; the streams mentioned flow into the Katherine R., not the Roper R. See Plate 31.

Of *E. pastoralis*: Adelaide River, in 1886, *Lea* (BM, NSW); figured in Maiden, Crit. Rev. *Eucalyptus* 3: Plate 105, Figure 8-9.

This is a characteristic tree of alluvial flats in parts of the north of the Northern Territory and adjacent parts of Western Australia. This is the first authentic record of the species from the latter State (map 20).

Juvenile leaves are not known; intermediate leaves have not been collected but from my recollection of them in the field they do not differ much from the adult leaves except in their larger size. The seeds are not known.

E. bigalerita was described from trees in immature bud. Accompanying the specimen preserved is a field label reading: Eucalyptus bigalerita/ferd Mueller/fertile plains on/the head of the/Roper/3-5 July 56, ferd Mueller/. According to Gregory's journal and map of the expedition, the days mentioned by Mueller were passed on and near the Dry River and what is now known as Darrinyan Creek, near their junction with what is now known as the King River; these streams drain into the Katherine River, not into the Roper River as was then supposed. Maiden evidently did not see this specimen; as mentioned in the discussion under *E. alba,* he stated that the type was a Fitzgerald specimen (collected 46 years after Mueller's name was published) and treated the name as a synonym of *E. platyphylla.* Mueller's specimen evidently represents the same form as the one described later by S. Moore as *E. pastoralis* from specimens in bud and flower, and the earlier name must be used.

Blakely and Jacobs (particularly Jacobs) suggested that the chief diagnostic character separating *E. bigalerita* and *E. platyphylla* lay in the well-developed pedicels of the latter, but there is practically no difference in this respect between the types of *E. platyphylla, E. pastoralis,* and *E. bigalerita.*

It is not without much hesitation that I have proposed the present treatment of *E. alba* and *E. bigalerita.* All observers agree that *E. bigalerita* is very distinctive in the field, although most of the comparisons have been made with the form of *E. alba* described as *E. platyphylla* var. *tintinnans,* with which it is often found in fairly close company — *E. alba* on the hillsides and *E. bigalerita* in the valleys between. The large, glossy, very green leaves are, however, equally unlike those of other forms of *E. alba*.

Series ARGYROPHYLLAE Blakely

35. **Eucalyptus apodophylla** Blakely & Jacobs in Blakely, Key Eucalypts 165 (1934)

A more or less completely deciduous tree with smooth, white, deciduous bark with a more or less powdery bloom; twigs more or less 4-angled, often sharply so or even more or less winged. Leaves sessile or nearly so, ovate or oblong or lanceolate-oblong, more or less cordate and amplexicaul at the base, from rather broadly to narrowly rounded at the apex and more or less apiculate to nearly acute, 6-18 cm. long, 2-6.5 cm. wide, 1.5-3 times as long as wide, strongly pruinose, but becoming more or less green and dull before falling, with 13-18 pairs of lateral veins at an angle of 40°-60° with the midrib and often somewhat irregular; intramarginal vein more or less confluent with the margin with a second one further in. Inflorescences of axillary, shortly pedunculate (peduncles 3-9 mm. long) umbels of 3-7 flowers on short and broad, flattened pedicels up to 2.5 mm. long. Buds pruinose, subglobular to obovoid, scarcely distinct from the pedicels, with 1 or 2 ribs, 5-6 mm. long, 4-4.5 mm. wide; operculum about as long as the calyx-tube, hemispherical, umbonate. Anthers versatile, obovate-oblong, with parallel cells opening in longitudinal slits, and a large dorsal gland. Fruit turbinate to cup-shaped, sometimes not distinct from the pedicels, with 1 or 2 faint ribs, a narrow rim, narrow convex disc, and 3 or 4 shortly exserted valves, in all 3-4 mm. long and 4-5 mm. wide.

NORTHERN TERRITORY.—Between Margaret R. and Mary R., about 13° 3′ S., 131° 32′ E., occasional on seasonally flooded, grassy flat, light grey soil, 52 m., 28.ix.1946, *Blake* 17084; Grove Hill, 13° 29′ S., 131° 33½′ E., open drainage flat, 70 m., 6.vii.1946, *Blake* 16346.

Type.—Jensen & Hill 345 from Pine Creek (NSW); fruits of this figured in Maiden, Crit. Rev. *Eucalyptus* 5: Plate 204, Figure 4, as *E. houseana* W. V. Fitzg. ex Maiden. *Paratype*: *Jacobs* 62 from near Stapleton (NSW, AFSC, BRI).

A species of restricted range on the alluvial flats and broad shallow drainage channels in the upper and middle parts of the watersheds of the Adelaide, Margaret, McKinlay, and Mary Rivers (map 22*A*).

E. apodophylla is readily distinguished by the smooth, white bark, the opposite, sessile or subsessile, more or less stem-clasping, ovate or oblong leaves, and the extreme glaucousness or pruinosity of the younger parts; the buds and fruits are not unlike those of some states of *E. alba*, but the two species are very different in foliage. Maiden assumed that specimens of *E. apodophylla* represented the juvenile state of *E. houseana* W. V. Fitzg. ex Maiden when he discussed the latter species in Crit. Rev. *Eucalyptus* 5: 291-4, 332, and Plate 204, Figures 2-4 (1921), but the leaves of *E. apodophylla* remain opposite, more or less sessile, and cordate throughout the life of the tree, while the adult leaves of *E. houseana* are alternate, lanceolate, and prominently petiolate. *E. houseana* is known only from the Kimberley Division of Western Australia (map 22*B*), and the fruits of it have not yet been described. I have seen three collections in herb. Sydney—*Fitzgerald* 1014 (type), *Fitzgerald* 1357 (paratype), both in bud and flower, and *Gardner* 1581, in old flower; one piece of the paratype has subsessile, ovate to oblong, more or less cordate leaves, and has buds. The type of *E. apodophylla* has fruit and young bud, but the leaves are not quite fully developed. In the paratype, ternate juvenile leaves are represented. The habit is shown in Plate 2, Figure 3 and Plate 3, Figure 1.

E. apodophylla var. *brachyphylla* Blakely & Jacobs (loc. cit., 166) appears to be a hybrid between *E. apodophylla* and *E. alba;* the type is *Jensen* 375 from Wandi (NSW, AFSC).

Series MYRTIFORMES Blakely

36. **Eucalyptus brachyandra** F. Muell. in J. Linn. Soc. (Bot.) 3: 97 (1859)

Deciduous small tree or shrub with rough bark; branchlets slender, angular. Leaves alternate or also opposite, rather thick, markedly paler on the under surface, ovate or oblong, very obtuse, about 5-8 cm. long, about 2-4 cm. wide, from a little less than twice up to thrice as long as wide, with about 15-20 pairs of primary lateral veins at an angle of about 55°-70° with the midrib; petioles 1-1.5 cm. long. Panicles small, terminal and in the upper axils; pedicels slender, 1.5-2 mm. long. Buds more or less pyriform with a broadly conical operculum nearly half as long as the calyx-tube, 2 mm. long and somewhat narrower. Anthers small, reniform or didymous, versatile, the cells somewhat oblique and opening nearly throughout in longitudinal slits that are nearly confluent at the apex. Fruits campanulate, thin, 2.5-3 mm. long and almost as wide with enclosed valves.

Type.—Rocky declivities of the Upper Victoria River, Dec. 1855, *F. Mueller* (MEL, NSW).

The outstanding characters appear to be the short, broad, and blunt leaves paler on the lower surface, the tiny buds, the didymous, versatile anthers opening in slits, and the very small, thin-walled fruits with included valves. Besides the type, I have seen three collections at Sydney from the Kimberley Division from Western Australia (Dillon's Springs, Oct. 1906, *Fitzgerald;* Artesian Range, Aug. 1905, *Fitzgerald;* Sunday Island, *Basedow* 115). Map 30*B* shows the distribution.

Series BUXEALES Blakely

37. **Eucalyptus patellaris** F. Muell. in J. Linn. Soc. (Bot.) 3: 84 (1859)

Tree to about 10 m. high with persistent, grey, shortly fibrous, superficially scaly bark, more evidently furrowed towards the base. Juvenile leaves opposite for up to at least 5 pairs, ovate to ovate-lanceolate, obtusely rounded, and more or less apiculate to more or less acute. Adult leaves lanceolate, more or less falcate, acute or acutely acuminate or more or less obtuse, about 12-24 cm. long and 2.2-4.5 cm. wide, 4-10 times as long as wide, about equally dull light green to subglaucous on both sides, with about 20-40 pairs of lateral veins at an angle of 30°-45° with the midrib and the intramarginal vein close to the edge, on petioles 1-2 cm. long. Panicles terminal and in the upper axils, shorter than the leaves; pedicels 6-11 mm. long, angular. Buds fusiform, somewhat acuminate, rather gradually narrowed to the pedicel, about 15 mm. long and 6 mm. wide; operculum conical and somewhat acuminate, as long as to slightly longer than the obconic, more or less distinctly 3- or 4-ribbed calyx-tube. Stamens all fertile; filaments not attenuated; anthers very small, subglobose, basifixed, with a dorsal gland, the cells opening laterally nearly throughout in rounded or somewhat elliptical pores. Fruits cup-shaped, cylindrical, or somewhat campanulate, shortly tapering to the pedicel, from 10 mm. long and 8 mm. wide up to 13 mm. long and 11 mm. wide, with a prominent depressed disc, which, together with the rim, is 2-3 mm. wide; valves 4, their tips flush to prominently exsert.

WESTERN AUSTRALIA.—Ten miles S. of Turner Station, on limestone near river, 11.vii.1949, *Perry* 2414. NORTHERN TERRITORY.—About NE. of Pine Creek, 13° 35′ S., 132° E., locally dominant in *Eucalyptus* forest on gentle slope, reddish, calcimorphic soil, about 150 m., 5.x.1946, *Blake* 17178; 40 miles SW. of Katherine, with *E. bigalerita* in open forest in shallow creek, 3.vi.1949, *Perry* 1997; 8.2 miles E. of Birdum, 20.vii.1947, *Perry* 399; 36.5 miles N. of Daly Waters, 19.vii.1947, *Perry* 392.

Type.—"Upper part of the Roper River, 3 July, 1856, *F. Mueller*" (K); drawing in MEL, NSW, part of the latter reproduced in Maiden, Crit. Rev. *Eucalyptus* 4: Plate 163, Figure 7. The locality given on the label is that quoted above, but on the date cited the party was working along the Dry River, a tributary of the Katherine River and one of the headwaters of the Daly River, in about 15° 20′ S. and about 133° 20′ E.

New for Western Australia; the localities cited above give the extent of its known range (map 25*A*). The species is sometimes fairly common on levees and alluvial flats.

The elongated, long-pedicelled, large buds and the relatively large fruits with a broad disc are both quite unlike those of any other "box", and the leaves are often longer than those of other species in the Northern Territory. In some respects the species resembles *E. leptophleba* from northern Queensland, but the intramarginal vein of the leaf tends to be slightly more distant from the margin, the fruits are widest at the rim with a broad disc and with the valves never included, and the bud is different. The smaller fruits are much like the larger fruits of *E. oligantha* and *E. argillacea,* but the broader disc is distinctive.

The type of *E. patellaris* consists of a single sheet at Kew with badly eaten leaves and with fruits and a bud that are badly pustulated. There is a careful drawing of this sheet at Melbourne and part of a similar drawing at Sydney has been published by Maiden as the figure cited above. Bentham (loc. cit., 244), particularly remarked upon the "diseased persistent bud", but it is apparently from this that Mueller described the operculum as patelliform, umbonate, and half as long as the calyx-tube ("much depressed, umbonate" according to Bentham). Well-developed buds and flowers were unknown until some were recently sent from Katherine by L. J. Phillips, and the description of these organs given above has been based on this collection.

The juvenile leaves were described by Blakely Key Eucalypts 238, as "opposite for 3 or more pairs, petiolate, narrow-lanceolate, acuminate". Those from my specimens are as described above; the smallest measures 4.3 cm. long and 1.9 cm. wide. Photographs of seedlings raised by Jacobs (S. 665) show leaves similar to mine, but smaller; they are opposite for at least 10 pairs.

38. **Eucalyptus leptophleba** F. Muell. in J. Linn. Soc. (Bot.) 3: 86 (1859)

E. stoneana F. M. Bail. in Qd. Agric. J. 23: 259, Plates 31-2 (1909).

Tree to about 15 m. high with persistent, grey or light grey, shortly fibrous, more or less fissured bark to the small branches; twigs slender, more or less pendulous. Juvenile leaves orbicular or ovate. Adult leaves dull, more or less subglaucous, not rigid, alternate, long-petiolate, broadly lanceolate to narrowly lanceolate, gradually acute or acuminate, tapering to the petiole, which is 1.6-3 cm. long, about 11-26 cm. long and 1.5-4.7 cm. wide, mostly 4-12 times as long as wide, finely and not prominently veined, with the intramarginal vein close to (0.3-1 mm. from) the edge and about 25-45 pairs of lateral veins at an angle of 35°-55° (mostly 40°-50°) with the midrib. Flowers in short, terminal, and subterminal panicles sometimes reduced to umbels; pedicels mostly 3-8 mm. long. Buds turbinate-obovoid, obtuse or apiculate or acuminate, gradually narrowed to the pedicels, 8-12 mm. long, 5-6 mm. wide; operculum hemispherical and minutely apiculate to acuminately conoid, from one-half to nearly as long as the calyx-tube. Anthers basifixed, ovoid, with distinct cells opening laterally in rounded pores. Fruit subsessile to shortly pedicellate, subabruptly narrowed to the pedicel, truncately ovoid or truncately ellipsoid, slightly narrowed upwards from about the middle, 9-12 mm. long, 7.5-9 mm. wide, with a thin rim and obscure disc, and 4 or 5 rather deeply enclosed valves.

Distribution.—Northern Queensland (map 25*B*).

Types.—Of *E. leptophleba*: Gilbert River, *F. Mueller* (MEL).

Of *E. stoneana*: Stannary Hills, Sept. 1909, *Bancroft* (BRI); figured by Bailey (loc. cit.). Specimens from the same locality and collector are figured in Maiden, Crit. Rev. *Eucalyptus* 5: Plate 201; they may be duplicate types or topotypes.

From the other boxes with large fruits (*E. patellaris, E. oligantha,* and some states of *E. argillacea*) this species is distinguished particularly by the relatively deeply sunken capsule and the fruit widest at or slightly below the middle.

The type of *E. leptophleba* consists merely of a fragmentary leaf and a few loose fruits. However, a number of specimens collected in the neighbourhood of the type locality by various persons has made possible a satisfactory interpretation of the species.

39. **Eucalyptus oligantha** Schau. in Walp. Repert. 2: 926 (1843)

E. hillii Maiden in J. Roy. Soc. N.S.W. 53: 63 (1919).

E. hillii Maiden var. *alleniana* Blakely & Jacobs in Blakely, Key Eucalypts 239 (1934).

A typical "box" with grey, compact, shortly fibrous, more or less fissured bark up to the twigs, more or less rugged towards the base and more scaly upwards; twigs terete and smooth. Leaves alternate on petioles of 2.5-7 cm., ovate or broadly ovate to somewhat rhomboid, obtuse to somewhat acuminate, from as long as wide up to twice as long as wide, mostly 10-20 cm. long and 5.5-12 cm. wide, rather prominently veined, with about 12-18 pairs of lateral veins at an angle of 30°-60° (mostly 40°-50°) with the midrib and with the intramarginal vein close to the margin and more or less confluent with it for some distance above the base; juvenile leaves rather similar, but opposite for a few pairs and with fewer lateral veins; intermediate leaves up to 20 cm. long and wide. Panicles terminal and in the upper axils, much shorter than the leaves; pedicels 3-9 mm. long. Buds obovoid, about 7-10 mm. long and 5-6 mm. wide; operculum about half as long as the calyx-tube, nearly hemispherical, apiculate. Anthers very small, basifixed, globular, opening in circular pores or short slits. Fruits on pedicels of 2-9 mm., truncately ovoid to shortly campanulate, about as wide or nearly as wide as long, 6-10 mm. long and 6-9.5 mm. wide, more or less glossy but also more or less wrinkled, slightly incurved to slightly expanded at the thin rim, with a depressed, narrow disc (rim with disc up to nearly 1.5 mm. wide but usually less) and 4 valves inserted below the orifice and their tips shortly included to shortly exserted.

NORTHERN TERRITORY.—Just W. of junction of Adelaide R. and Margaret R., with *E. grandifolia* on creek flat, about 60 m., 13.ix.1946, *Blake* 16991; SSE. of Brocks Creek, "orchard country" with chiefly *Eucalyptus foelscheana*, hard, shallow, red soil, 116 m., 29.vi.1946, *Blake* 16221; NE. of Pine Creek, 13° 40′ S., 131° 56′ E., edge of shallow drainage flat in mixed *Eucalyptus* forest, about 135 m., 5.x.1946 *Blake* 17179.

Types.—Of *E. oligantha*: Copeland Island, Mountmorris Bay, *Cunningham* 250/1818 (K); figured in Maiden, Crit. Rev. *Eucalyptus* 2: Plate 64, Figure 3 (isotype).

Of *E. hillii*: *Hill* 468 from Bathurst Island (NSW); figured in Maiden, op. cit., 5: Plate 203 and in this paper, Plate 32, Figure 1.

Of *E. hillii* var. *alleniana*: *Jacobs* 58, from 6 miles S. of Batchelor Farm (NSW, AFSC, BRI); figured in Plate 32, Figure 3 and Plate 30, Figure 39.

Known only from a restricted area in the north-western part of the Northern Territory (map 30*A*).

E. oligantha was described from a flowering specimen. There is a duplicate at Kew, of which a drawing was published by Maiden (loc. cit.); I have also seen a few stamens at Sydney. *E. hillii* was likewise described from flowering material only, while *E. hillii* var. *alleniana* was based on specimens in relatively new leaf with fruits and (to judge from the description) some immature buds, but no buds are present on the sheets at Sydney and Brisbane. *Jacobs* 41 from Bathurst Island is in fruit; since it comes from the type locality of *E. hillii* and has foliage closely agreeing with the type material it may be accepted as truly representing the fruiting stage of this form. *Jacobs* 36 from the neighbouring Melville Island has some larger fruits recalling those of *E. patellaris*.

Blake 16991, 16221, and 17179 certainly appear to represent one and the same species, although there are slight differences between them. Except for their slightly smaller size, the fruits of *Blake* 16221 match those of *Jacobs* 41 very closely (Plate 30, Figs. 40, 41); the older leaves resemble those of this collection and some of those of *Blake* 16991, but the younger ones are very like some of those on *Jacobs* 58. *Blake* 17179 has fruits with flush to distinctly exsert valves; the fruits with exsert valves match those of the type of *E. hillii* var. *alleniana* (Plate 30, Figs. 38, 39), while the leaves agree in form and venation with this collection but are even younger. Besides juvenile and intermediate foliage, *Blake* 16991 consists of numerous sheets from a single tree in bud and all stages of flower and fruit and fully developed leaves; part of this collection agrees well with the figure of the duplicate type of *E. oligantha* and part of it agrees well with the type of *E. hillii* (cf. Plate 33 and Plate 32, Fig. 1, and Maiden's figure cited above), while the fruits agree well with some from *Blake* 17179 (cf. Plate 30, Figs. 37, 38). This collection therefore shows that there is no discontinuity between the forms described as *E. oligantha, E. hillii,* and *E. hillii* var. *alleniana*.

E. oligantha is known only from the seven collections discussed above. From the other "boxes" it is distinguished by the more or less deltoid or rhomboid, long-petiolate, often very large leaves with only 12-18 pairs of lateral veins and the firm, cup-shaped fruits with slightly included to distinctly exserted valves. The larger fruits resemble the smaller ones of *E. patellaris* but both disc and rim are narrower. In foliage, the species closely resembles some states of *E. alba, E. bigalerita,* and *E. grandifolia,* but the leaves are always alternate, the intramarginal vein is more regular and closer to the margin and more or less confluent with it for some distance above the base, and the lateral veins are sometimes more numerous; *E. bigalerita* has frequently a second intramarginal vein, and *E. grandifolia* has mostly shorter petioles.

E. fitzgeraldii Blakely (loc. cit., 239) from the Kimberley Division of Western Australia is the only other "box" that at all resembles *E.*

oligantha in appearance. The only material available has been the very scrappy type at Sydney, collected by Fitzgerald between Table Top and Artesian Range and figured in Maiden, op. cit., 2: Plate 64, Figure 4 under *E. oligantha.* The specimen carries flowers and immature fruits and a few imperfect leaves. The longer calyx-tube somewhat contracted below a slightly spreading rim is rather different from what has been so far observed in *E. oligantha,* but the "more orbicular" leaves stressed by Blakely seem to have no significance in view of their damaged condition and the variation observed on individual branches of *E. oligantha.* However, to judge from the remarks of Gardner in For. Dep. W. Aust. Bull. No. 32: 76 (1923), the bark of the Kimberley tree differs much from that of the tree of the Northern Territory.

40. **Eucalyptus argillacea** W. V. Fitzg. in Maiden, Crit. Rev. *Eucalyptus* 4: 132, Plate 147, Fig. 8 (1918)

E. leucophylla Domin in Bibl. Bot. 89: 464 (1928); *syn. nov.*

E. tropica Cambage ex Maiden, Crit. Rev. *Eucalyptus* 8: 6, Plate 289, Fig. 3-4 (1929); *syn. nov.*

Tree, sometimes small and shrubby, with grey, closely fissured, compact, shortly fibrous bark towards the base and sometimes throughout, but commonly with a conspicuous amount of smooth brown bark on the upper part; young growth sometimes more or less pruinose. Juvenile leaves petiolate, opposite for several pairs, lanceolate. Adult leaves alternate, prominently petiolate, concolorous, green and shining to whitish and dull, lanceolate, more or less obtuse and apiculate to acute or acuminate, more or less falcate, about 8-14 cm. long and 1.0-3.7 cm. wide, 4-12 times as long as wide, with a large number (about 30 or more pairs) of lateral veins at an angle of 50°-65° with the midrib, all the veins very faint; petioles 5-13 mm. long. Inflorescences terminal and in the upper axils, of compact, more or less pyramidal panicles usually shorter than the leaves; umbels 4-6-flowered; pedicels 4-5 mm. long. Buds turbinate or somewhat pyriform, rather gradually tapering into the pedicel, 6-8 mm. long and 4-5 mm. wide; operculum conical or rounded and sometimes umbonate, about half as long as the calyx-tube. Stamens all fertile; anthers basifixed, broadly ovoid-oblong and somewhat cordate, with a small terminal gland, the cells distinct and opening throughout their length in broad lateral slits contiguous at the top, but not confluent. Fruits more or less turbinate, distinct from their pedicels, more or less striate and more or less wrinkled, 4.5-9 mm. long, 4.5-6 mm. wide, with 4 (rarely 5) more or less exserted valves; rim slightly convex, together with the narrow, more or less depressed disc up to 1 mm. wide.

WESTERN AUSTRALIA.—Seven miles N. of Hall's Creek, dominant tree on small, alluvial flat, 16.vii.1949, *Perry* 2500. NORTHERN TERRITORY.—Seven miles SW. of Birrimbah Station, fringe between heavy soil plain and lateritic podsol, 5.vi.1949, *Perry* 2055; 40 miles E. of Limbunya Station, red lateritic soil, dominant tree, 28.vi.1949, *Perry* 2292; 24.7 miles N. of Daly Waters, 19.vii.1947, *Perry* 391; 4.1 miles E. of "Dunmarra", 15.vii.1947, *Perry* 380; on Nutwood Downs Station, 16° 5′ S., 134° 26′ E., in *Eucalyptus-Petalostigma* very open grassy forest, 201 m., 2.v.1947, *Blake* 17603; 16° 25′ S., 134° 59′ E., dominant tree in open forest, grey, hard, sandy soil, 173 m., 4.v.1947, *Blake* 17628; 33 miles S. of McArthur River Station, codominant with *E. confertiflora* in open forest with *Heteropogon contortus*, 23.vii.1948, *Perry* 1688; 42.1 miles N. of Tennant Creek, 1.vii.1947, *Perry* 172; Carrara Ck., 18° 52′ S., 137° 46′ E., forming an open community with *Triodia pungens* on broken limestone slope towards the creek, with little soil, 290 m., 25.v.1947, *Blake* 17927; W. of Soudan Station, 19° 54′ S., 136° 21′ E., scattered among *Triodia* sp. on very gentle slope, reddish, sandy soil, 302 m., 20.v.1947, *Blake* 17898. QUEENSLAND.—Eight miles S. of Mount Isa, shallow soil on slates, 8.v.1948, *Perry* 768; about 35 miles ESE. of Cloncurry, near Fullarton R., associated with *Triodia pungens* on a stony ridge, 5.xi.1946, *Blake* 17372.

Types.—Of *E. argillacea*: *Fitzgerald* 962 from Mount House, W.A. (NSW); figured in Maiden (loc. cit.).

Of *E. leucophylla*: dry spinifex hills near Cloncurry, Feb. 1910, *Domin* (hb. Domin), not seen; topotypes: *Hubbard* 7337, *Blake* 17372 (BRI) (*Blake* 10088 agrees with the description and is from the same locality, but not from stony hills).

Of *E. tropica*: *Cambage* 4163 from Corella R., N. of Cloncurry (NSW); figured in Maiden (loc. cit.).

Widely spread in a variety of habitats from the Kimberley Division of Western Australia across to north-west Queensland, chiefly in the drier regions (map 20).

Up to the present, *E. argillacea* has always been treated as a Western Australian endemic. Fitzgerald described both flowers and fruit, but I have not seen the latter; Maiden figured them but stated that they were old and "evidently gathered at the foot of the tree".

Both *E. leucophylla* and *E. tropica* were described from fruiting specimens from localities about 25 miles apart. From the several collections made by myself and others in this area, there seems no doubt that Domin's tree is the common and widespread "box" of the area. In his description, Domin laid considerable stress on the pale-coloured leaves and they are frequently so glaucous as to dry nearly white; often, however, the leaves are quite green. Blakely considered *E. tropica* was distinct from *E. leucophylla,* largely because (as he explained in correspondence) of the colour of the leaves, but an examination of the type of *E. tropica* has convinced me that it represents the common tree of Domin's locality and the two names must be regarded as synonymous. Maiden (loc. cit.) cited Cambage as the author of *E. tropica,* with two references to *Proc. Roy. Soc. N.S.W.;* in the first passage cited (**49**: 425), Cambage described in a general way some trees seen during a journey from Normanton to Cloncurry, but no name was applied to them; the second reference (vol. **61** . . .) can apply only to a name without description on p. xix, so that the first valid publication of the name is by Maiden (loc. cit.).

Most of the specimens from Queensland closely resemble the type of *E. argillacea* in facies. *Hubbard* 7377 from Duchess (SW. of Cloncurry) is the only specimen seen which carries buds, flowers, and fruits. Some of these fruits (and some from *Blake* 10088) closely resemble Maiden's figure for *E. argillacea* and the buds and flowers (as well as those on one specimen collected near Camooweal by de Lestang) agree with those on Fitzgerald's specimen.

The anthers vary slightly in length on each of the five flowering specimens seen. The fruits are variable in size and form and in the degree to which the valves protrude; in general they recall those of *E. patellaris* on a smaller scale, while the buds are rather like those of *E. leptophleba*. *E. argillacea* differs from both these species in having smaller leaves with more oblique, often quite indistinct veins. *E. microneura* Maiden & Blakely from northern Queensland is closely allied to *E. argillacea;* its twigs, buds, and fruits are more intensively and more persistently pruinose, the juvenile leaves are narrower, the adult leaves are of rather thinner texture with the intramarginal vein more distant from the margin, the lateral veins make a more acute angle (40°-50°) with the midrib, and the anther cells are slightly spreading (not parallel).

The amount of smooth bark on trees of *E. argillacea* is very variable, and is sometimes quite inconspicuous.

41. **Eucalyptus microtheca** F. Muell. in J. Linn. Soc. (Bot.) 3: 87 (1859)

E. raveretiana F. Muell. var. *jerichoensis* Domin in Bibl. Bot. 89: 464 (1928).

E. microtheca F. Muell. var. *cymbaliformis* Blakely & Jacobs in Blakely, Key Eucalypts 245 (1934).

E. coolabah Blakely & Jacobs, loc. cit., 245.

E. coolabah Blakely & Jacobs var. *arida* Blakely, Key Eucalypts 246 (1934).

Tree, usually more or less crooked or irregular and sometimes branched low down, with commonly a broad spreading crown; bark grey, shortly fibrous, rough, more or less scaly to rugged and deeply furrowed towards the base, more scaly upwards; upper part of tree usually with a variable amount of smooth, pale grey or whitish, deciduous bark, sometimes confined to the twigs, sometimes extending down to the trunk, and sometimes — in extreme cases — extending practically to ground-level; twigs slender, more or less angular. Leaves lanceolate to somewhat oblong, obtuse to more or less acute or acuminate, straight or falcate, about 6-20 cm. long and 0.7-3 cm. wide, commonly 5-10 times as long as wide (rarely wider or narrower), concolorous and dull, with the midrib alone usually prominent, the lateral veins in about 30-40 pairs at an angle of 40°-60° with the midrib, on petioles 0.8-2.0 cm. long; juvenile leaves opposite for several pairs, petiolate, lanceolate, with fewer veins. Panicles small, terminal and in the upper axils; pedicels short, mostly shorter than the calyx-tube. Buds nearly ellipsoid or somewhat ovoid, from 4 mm. long and 3 mm. wide up to 6 mm. long and 4 mm. wide; operculum about as long as (rarely distinctly longer or shorter than) the calyx-tube, shortly apiculate or shortly acuminate. Anthers basifixed, subglobose, with distinct cells opening almost throughout their length in broad slits or elliptical pores. Fruits subsessile to distinctly pedicellate, as broad as or broader than long with a hemispherical or broadly turbinate or almost saucer-shaped calyx-tube with an incurved or variously expanded rim, and 3 or 4 broad valves more or less exserted and often occupying about half the height of the fruit, which varies from 3 mm. long and wide up to 4.5 mm. long and 5.5 mm. wide; disc small and obscure or up to nearly 1 mm. wide.

WESTERN AUSTRALIA.—Twenty miles S. of Nicholson Station, near salty creek, 13.vii.1949, *Perry* 2433; 6 miles NE. of Gordon Downs Station, dominant tree on lateritic flat, 13.vii.1949, *Perry* 2445. NORTHERN TERRITORY.—Near (W. of) junction of Douglas R. with Daly R., in shallow depression, 41 m., 16.vii.1946, *Blake* 16475; near Katherine, shallow depressions in *Eucalyptus* forest, grey soil, about 107 m., 9.x.1946, *Blake* 17189; near Katherine, 14° 22½′ S., 132° 23′ E., lower part of gentle slope carrying scrub of *Melaleuca minutifolia*, about 110 m., 13.x.1946, *Blake* 17219; Kathleen Falls, Flora R., fringing forest of *Melaleuca* spp. etc., 104 m., 16.x.1946, *Blake* 17231; 7 miles SE. of Birrindudu Station, edge of swamps, 6.vii.1949, *Perry* 2367; near Wave Hill Police Station, near small creek, 25.vi.1949, *Perry* 2254; 35 miles N. of Helen Springs Station, codominant with *Tristania* sp. on yellow-grey flat with *Eulalia fulva*, 15.viii.1948, *Perry* 1896; 34.1 miles N. of Helen Springs Station, 6.vii.1947, *Perry* 224; 32.2 miles N. of Tennant Creek, 1.vii.1947, *Perry* 162; 25 miles N. of Tennant Creek, on yellow-grey flat with *Acacia cuthbertsonii*, 26.iv.1948, *Perry* 647; 25 miles N. of Tennant Creek, red upland laterite soil with *Hakea*, *Acacia*, and *Triodia* scrubby woodland, 26.iv.1948, *Perry* 648; 13 miles NE. of Tennant Creek, flat alluvial plain, 24.iv.1948, *Perry* 561; McArthur R., 16° 46′ S., 135° 45′ E., common on alluvial flats, 76-78 m., 14.v.1947, *Blake* 17767; half way between Brunette Downs and Rockhampton Downs, pale grey, ashy soil plain, scattered trees with more or less *Chenopodium auricomum*, 197 m., 18.v.1947, *Blake* 17836; "Frewena", 19° 30′ S., 135° 28′ E., broad, shallow depression, reddish, very sandy soil, 219 m., the dominant tree, 20.v.1947, *Blake* 17882; "Frewena", 19° 30′ S., 135° 28′ E., broad, shallow depression, reddish, very sandy soil, 219 m., locally dominant tree in open dwarf tree-*Plectrachne schinzii* community, 3.xi.1946, *Blake* 17365; on road 22 miles E. of "Frewena" in scrubby desert country, 29.iv.1948, *Perry* 672; near Soudan Station, dominant tree on slightly truncated laterite desert, 30.iv.1948, *Perry* 685; along channels of Playford R., 18° 52′ S., 137° 10′ E., 293 m., 22.v.1947, *Blake* 17922; banks of Eastern Ck., 19° 1′ S., 137° 12′ E., 290 m., 22.v.1947, *Blake* 17921; 60 miles W. of Gallipoli Station, 14.vi.1948, *Perry* 1539; 7 miles W. of Gallipoli Station, edge of swamp with *Chenopodium auricomum*, 15.vi.1948, *Perry* 1564; 12.5 miles W. of Alroy Downs Station, dominant tree on lateritic yellow-grey flat, 30.vi.1948, *Perry* 1571; Austral Downs Station, channels of Georgina R., 195 m., 30.v.1947, *Blake* 17971; 8 miles WSW. of Lake Nash Station, with *Triodia* sp. on sandy desert soil, 20.v.1948, *Perry* 868. QUEENSLAND.—Burke district: 37.4 miles N. of Lawn Hill Station, codominant with *E. polycarpa* in open forest on levee, 31.v.1948, *Perry* 1114; 9 miles N. of Lawn Hill Station, slope to creek, 31.v.1948, *Perry* 1097; near (N. of) Camooweal, with *Acacia cambagei* in a depression with heavily gravelled, grey soil, 26.v.1947, *Blake* 17932; 30 miles SSE. of Camooweal, with *Triodia* sp. and *Eulalia fulva* on alkaline, heavy clay alluvial soil, 3.v.1948, *Perry* 725; 33 miles SSE. of Camooweal, with *Triodia* sp. and *Eulalia fulva* on alkaline, heavy clay alluvial soil, 3.v.1948, *Perry* 726; 50 miles SSE. of Camooweal, along small creek in alluvial flat, associated with *Acacia farnesiana* and *Aristida* spp., 4.v.1948, *Perry* 728. Gregory North district: 2.7 miles NW. of Oban Station, associated with *Acacia* spp. and *Aristida* spp. on red, sandy alluvial desert, 10.v.1948, *Perry* 796; ½ mile E. of Carandotta Station, near creek, 12.v.1948, *Perry* 809; same locality and date, *Perry* 810; same locality and date, *Perry* 811.

Types.—Of *E. microtheca*: Victoria River, Dec. 1855, *F. Mueller* (MEL, NSW); Plate 34; Plate 30, Figure 20.

Of *E. microtheca* var. *cymbaliformis*: *Jacobs* 141 from Newcastle Waters (NSW, AFSC, BRI); Plate 30, Figure 26.

Of *E. coolabah*: "Figs. 16, 18*a*-18*c*, 19*a*, 19*b* of Plate 52" in Maiden, Crit. Rev. *Eucalyptus* 2.

Of *E. coolabah* var. *arida*: *Basedow* 17 (Nov. 1919) from Kopperamana, Cooper's Creek, S.A. (NSW, BRI); Plate 30, Figure 25.

Of *E. raveretiana* var. *jerichoensis*: Jericho, *Domin* (not seen).

Widely spread throughout the inland parts of the continent on ground subject to seasonal flooding (map 24).

The proportion of smooth to rough bark varies from entirely rough to almost entirely smooth, the proportion being uncorrelated with other characters. The fruits vary considerably, even on the same tree (see Plate 30, Figs. 20-36, particularly Figs. 30 and 32), but their small size with the relatively short and broad calyx-tube and the broad, usually strongly exserted valves are usually fairly characteristic. Somewhat cup-shaped fruits with short valves are found on some trees, as in *Blake* 16475, 17189, 17767 (Plate 30, Fig. 22).

In the protologue, *E. microtheca* was stated to be not rare in Tropical New Holland, on the more fertile plains; on pp. 82 and 100, Mueller implied that the operculum was unknown; in the description, the branches were said to decorticate in the upper part and were then ashy and smooth. Only one herbarium specimen has been located at Melbourne that could have been examined and labelled by Mueller prior to the publication of the description. The label originally bore the words: Boxtree/E. microtheca F.M./Victoria River/Dec. 55 ferd. Mueller/; at a later date Mueller wrote above these words: Eucalyptus brachypoda Turcz.; and at a later date "Bth. non" were written in before "Turcz." However, this specimen is in excellent bud and flower, with a packet of loose fruits; part of it is shown in Plate 34 and Plate 30, Figure 20. In Sydney there is a sheet, ex herb. Hooker, with a specimen with one immature fruit and label reading: Eucalyptus microtheca/ferd. Mueller/Victoria River/ferd. Mueller/ in Mueller's writing; this appears to be part of the same collection as the Melbourne specimen. A search through the material at Kew would be necessary before it could be decided whether other collections should be considered in selecting the type; but since the specimens seen agree with Mueller's description and other data except for the additional presence of buds and flowers that cannot be referred to any other species, and since the specimens represent the species generally called *E. microtheca* even in the most restricted sense, there seems every justification for regarding the specimens as truly representing Mueller's species with the status of at least syntype, if not actually isotype. (Miss M. B. Tindale has subsequently searched through the material at Kew for specimens that might be important in typifying the name. Only two sheets of interest were found, photographs of which are now at Brisbane, but neither has any special claim; one from Victoria River, June 1856, is in bud, flower, and old flower; the other from between the Flinders and Lynd Rivers, probably belongs to another species, but I think Bentham was wrong in determining it as *E. crebra* F. Muell.)

E. coolabah was typified in Plate 52, Figures 18-19 of Maiden's "Critical Revision", and Figure 21 was also cited with the original description. From the protologue and Jacobs's more extended discussion in Surv. Genus *Eucalyptus* in North. Territ. 51 and 64, *E. coolabah* is distinguishable from *E. microtheca* by the bark being smooth and deciduous on the upper part of the tree (Jacobs in particular stated that the bark is rough and persistent throughout in *E. microtheca*), the flatter fruits with strongly exserted valves, and the red wood without the fine white threads of the very dark brown to nearly black wood of *E. microtheca*. But on trees with fruits closely matching those of the type of *E. microtheca*, I have noted considerable variation in the bark, some having persistent rough bark up to the twigs (e.g. *Blake* 16475), others having smooth, deciduous bark extending downwards to the main branches (*Blake* 17971). As to the fruits themselves, intermediate shapes are found between the form characteristic of the type of *E. microtheca* and the form characteristic of *E. coolabah* (Plate 30, Figs. 20-36, particularly Figs. 20, 30, 32). Very little variation has been noticed in the buds; the rhomboidal outline shown in Maiden (loc. cit., Fig. 19*a*) is not noticeable on the specimen from which the figure was drawn (Bourke District, *O. C. McDougall*), but the opercula on this specimen are longer than usual. There is a marked difference between the woods of the extreme types, but I have not examined many specimens and *Blake* 17922 has dark wood with the white threads of *E. microtheca* and fruits resembling the type of *E. coolabah* as closely as they do those of *E. microtheca* (cf. Plate 30, Figs. 28, 20, and 30). In 1948, Perry collected wood and herbarium specimens from 11 trees from a number of widely scattered localities. The wood specimens have been examined by Dr. H. E. Dadswell, of the Division of Forest Products, C.S.I.R.O., Melbourne, but his determinations based on the woods cannot be reconciled with Perry's field determinations based chiefly on the bark, nor with my earlier determinations based on the fruits. In other words, bark, wood, and fruits appear to vary independently of one another, while other characters remain fairly constant. On the evidence available, it seems that *E. coolabah* must be regarded as a synonym of *E. microtheca*.

E. microtheca var. *cymbaliformis* was founded on specimens from trees growing with the "typical" form at Newcastle Waters. It is characterized by having a relatively broad, flat rim to the fruits, and from the type alone it appears a very distinctive form; however, it is connected with "typical" *E. microtheca* by intermediates, different stages being found on the same tree as in *Blake* 17219, 17922, 17971 (see also Plate 30, Figs. 28 and 32).

In its extreme form, *E. coolabah* var. *arida* is also quite distinctive. The type has prominently pedicellate and rather large, broadly turbinate fruits with nearly flush valves (Plate 30, Fig. 25); it is nearly matched by *Perry* 868 (Plate 30, Fig. 35). *Perry* 561, 647, 648, 685, 1571 and *Blake* 17365, 17822 (Plate 30, Fig. 36) are more or less comparable, but differ in having shorter pedicels or more cup-shaped fruits or both. The specimens are from shrubs or small, shrubby trees with the bark almost or entirely smooth and white, and thickly coriaceous leaves. But the leaves are quite like those of *Blake* 17836 (which is otherwise fairly characteristic *E. microtheca* — cf. Plate 30, Fig. 23), there is nothing peculiar in the shape of the fruits though they are more often four-celled, and there is a gradation in size between them and those of characteristic *E. microtheca*.

The type of *E. raveretiana* var. *jerichoensis* has not been seen, but Domin stated that the tree formed stands along the creek at Jericho (central Queensland); it was a "box-tree" with long and narrow leaves scarcely narrowed at the apex and depressed-globose fruits with four broadly deltoid, exserted valves rather longer than the calyx-tube. These characters agree well with those of *E. microtheca* (of which there are specimens from Jericho at Brisbane), but with nothing else known from the area. (*E. raveretiana* appears to be restricted to areas near the coast from about the same latitude northwards; fruiting specimens have a superficial resemblance to some forms of *E. microtheca*.)

Bentham's misidentification of *E. brachypoda* Turcz. has been discussed under *E. brevifolia*.

To judge from its resemblances and distribution, *E. rivularis* Blakely Key Eucalypts 253 appears to be a hybrid between *E. microtheca* and *E. melanophloia* F. Muell. Blakely remarked upon the resemblance to and its association with these species in the protologue. So far as I have seen this form in the field, it occurs as occasional individuals on or near stream banks amongst *E. microtheca* with *E. melanophloia* close by.

The following collection appears to represent a hybrid between *E. microtheca* and *E. pruinosa* Schau., both of which grow in the same locality:

QUEENSLAND.—Six miles NW. of Yelvertoft Station, on edge of heavy clay alluvial plain, 12.vi.1948, *Perry* 1462 (straggly, grey tree 20 ft. high with rough, grey, fibrous bark; wood fizzes with dilute acid).

The leaves of this collection have short petioles and an intramarginal vein well removed from the margin, and they tend to be both opposite and cordate; the fruits are more or less cup-shaped and intermediate in form between those of the suspected parents, but the valves are more or less flush.

42. **Eucalyptus tectifica** F. Muell. in J. Linn. Soc. (Bot.) 3: 92 (1859)

E. spenceriana Maiden in Ewart & Davies, Fl. North. Territ. 307 (1917).

A typical "box" up to 12 m. high with rough, grey, shortly fibrous, more or less scaly bark up to the twigs and more or less completely deciduous leaves; twigs slender, more or less terete. Adult leaves lanceolate or broadly lanceolate, mostly 8-16 cm. long and 1-4.5 cm. wide, mostly more than 3 and up to 9 times as long as wide, more or less acute or acuminate or rarely more or less obtuse, more or less cuneate at the base, straight or falcate, dull on both sides and commonly more or less glaucous, the venation fine with between 20 and 30 pairs of lateral veins at an angle of 45°-55° with the midrib and an intramarginal vein more or less contiguous to the margin in the narrow leaves but up to 0.5 mm. distant in the broader ones; petioles 1-2.5 cm. long. Inflorescences terminal and in the upper axils, consisting of more or less pyramidal panicles shorter than the leaves, mostly reduced to racemes of slenderly pedunculate, 3-6-flowered umbels. Buds pyriform-obovoid, attenuated to pedicels from about as long as to distinctly shorter than the calyx-tube, from 5 mm. long and 4 mm. wide up to 6 mm. long and 5 mm. wide; operculum subconical and shortly acuminate, rather shorter than the calyx-tube. Anthers basifixed, subglobose or somewhat reniform, opening in pores which are subterminal or more or less distinctly lateral, but shorter than the cells. Fruits pedicellate, very thin and fragile, cup-shaped but sometimes slightly contracted or incurved at the orifice, from 4 mm. long and wide up to 6 mm. long and 5 mm. wide, with a very thin rim, an obscure disc, and 3 or 4 slightly included to slightly exserted valves.

WESTERN AUSTRALIA.—Argyle-Newry road, near small, dry creek, 8.viii.1949, *Perry* 2681. NORTHERN TERRITORY.—SE. of mouth of Daly R., 13° 27′ S., 130° 30′ E., dominant tree in mixed *Eucalyptus* forest, 36 m., 27.vii.1946, *Blake* 16646; near Edith R., NW. of Katherine, with *E. latifolia* and *E. dichromophloia* in open *Eucalyptus* forest, stony, hard soil, 24.vi.1946, *Blake* 16094; 25 miles SW. of Auvergne Station, dominant tree on levee, 10.viii.1949, *Perry* 2685; 20 miles NW. of Birrimbah Station, lateritic flat with *Melaleuca leucadendra,* 4.vi.1949, *Perry* 2054; 7 miles SW. of Katherine, parkland with *Chrysopogon,* 2.vi.1949, *Perry* 1966; 40 miles SW. of Katherine, open forest on limestone soil flat, 3.vi.1949, *Perry* 1996; 20 miles N. of McArthur River Station, on levee, 26.vii.1948, *Perry* 1760; Settlement Creek, 10 miles NE. of Woologorang Station, levee of creek, 2.vi.1948, *Perry* 1191.

Types.—Of *E. tectifica*: McArthur River, *F. Mueller* (K, photographs in NSW) ; see below.

Of *E. spenceriana*: *Jensen* 346 from Burrundie (NSW) ; figured in Maiden, Crit. Rev. *Eucalyptus* 4: Plate 157, Figure 2.

A species widely spread in northern Australia, chiefly on the slopes of the hills, but sometimes on levees (map 26). The habit is shown in Plate 2, Figure 2 and Plate 1, Figure 1.

This species is chiefly distinguished by the following combination of characters: "box" bark; lanceolate leaves with 20-30 pairs of lateral veins; porous dehiscence of the anthers; and the small, frail, cup-shaped fruits with the tips of the valves from slightly below to about flush with the orifice (rarely distinctly exserted). It is very close to *E. microtheca* from which it is distinguished by the somewhat shorter anthers dehiscing in pores rather than in slits, the more deeply cup-shaped and sometimes larger fruit, of which the valves are not much exserted but commonly flush or included, and the fewer lateral veins to the commonly broader or shorter leaves that sometimes have longer petioles, and the operculum is sometimes distinctly shorter than the calyx-tube; some specimens with narrow leaves and small fruits are difficult to distinguish. *Perry* 1760 has fruits with rather distinctly exserted valves, but they are much weathered; *Perry* 2681 has some leaves with some lateral veins at an angle of only 40° with the midrib and some with the intramarginal vein nearly 1 mm. from the edge, while the fruits are 6.5-7 mm. long and 6-7 mm. wide.

According to the protologue, *E. tectifica* was founded on trees from grassy valleys towards the source of the McArthur River. It is clear that only one specimen in immature bud was collected and that the description of the inflorescence (and probably also of the leaves) was based entirely on this. The specimen was sent to Hooker and the application of the name soon became doubtful. Bentham (loc. cit., 243) treated the name as a synonym of *E. alba* Reinw. ex Bl.; Mueller, in Eucalyptogr. dec. 4 (1879) under *E. alba,* was unwilling to agree with this because of the rough bark and paniculate inflorescence—an elaboration of his doubt previously expressed in *Pap. Pl.* 1: 9 (1875)—but appears to have made no further reference to the name. Maiden at first (op. cit. 3: 92, 95) appears to have accepted Bentham's synonymy, although he quoted Mueller's remarks; later, in 1929 (op. cit. 8: 103), he treated it as distinct from *E. alba* because of the description of the bark and buds, and stated there that it appeared to be allied to *E. spenceriana* Maiden and *E. hillii* Maiden. Blakely (loc. cit., 240 (1934)) accepted Maiden's later opinion by treating it as a distinct species. In 1936, two excellent photographs of the type were sent to Sydney from Kew, and I have been able to make a detailed study of these. One of them shows the entire sheet about half natural size while the other shows the actual specimen slightly more than half (0.573) natural size. The sheet bears a label written up by Mueller as follows: Eucalyptus tectifica/ferd Mueller/M'Arthur River/Gulf of Carp./5 Aug 56. ferd Mueller/. Above this is one of Bentham's determination slips for Flora Australiensis with the annotation of the sheet: E. alba Reinw./iii.p.243./. Above this *E. alba* has also been written on the sheet (in pencil?) by Bentham. Near the annotation has been written: Dr. Mueller/1857/, evidently a reference to the origin and date of receipt of the specimen. The sheet also bears a stamp reading: HERBARIUM HOOKERIANUM 1867; this refers to the date when Hooker's herbarium was transferred to Kew.

From the date of collection and Gregory's journal of the expedition, it appears that the specimen was collected close to the site of the present homestead of McArthur Station, which is about 16° 47′ S. and 136° 8′ E. The photographs are such that it is possible to study even the finer details of the venation of the leaves and of the bud and the operculum. It is clear that Mueller's specimen represents the species later described by

Maiden as *E. spenceriana.* Some pieces of *Blake* 16646 are an extraordinarily close match for the photograph, but they were collected a long way from Mueller's locality. *Perry* 1760 was collected close to the type locality, but it is in fruit only; some leaves of it closely match the narrower ones on the photograph.

Two other species with rough, grey bark and similar inflorescences are known from the neighbourhood of the McArthur River. These are *E. argillacea* W. V. Fitzg. and *E. microtheca* F. Muell., but the leaves of both of these have more numerous veins and are mostly much narrower with shorter petioles, while those of *E. argillacea* are also more coriaceous than those described for *E. tectifica,* with the veins at a more obtuse angle and its buds have a relatively much shorter operculum.

43. **Eucalyptus cyanoclada** Blakely, Key Eucalypts 242 (1934)

Tree with rough, grey, persistent, "box" bark throughout; twigs very slender, yellowish, bluish, or more or less pruinose. Juvenile and intermediate leaves not seen. Adult leaves alternate, petiolate, more or less glaucous and about the same colour on both sides, lanceolate, more or less falcate, obtuse to more or less acute or acuminate, 4-6 times as long as broad, 7-16 cm. long and 1.5-3 cm. wide, oblique at the base and somewhat abruptly narrowed to a petiole of 1-2.5 cm., finely but rather prominently veined with the intramarginal vein rather distant (about 0.7-1.5 mm.) from the margin, with about 18-26 pairs of lateral veins at an angle of 50°-60° with the midrib, with several secondary lateral veins, and loosely reticulate. Panicles terminal and in the upper axils, shorter than the leaves, with slender or very slender branches and pedicels; pedicels up to 5 mm. long, sometimes rudimentary. Buds turbinate-obovoid to somewhat pyriform, sharply distinct from the pedicels, minutely wrinkled, 4-4.5 mm. long, about 4 mm. wide; operculum patelliform to nearly hemispherical, narrower than the calyx-tube, and from rather less to rather more than half as long as it. Stamens all fertile, anthers basifixed, sometimes oblique on the filaments, suboblong, opening nearly throughout the length of the cells in large, oval pores or short, broad slits. Fruit very thin, campanulate-urceolate, sharply distinct from the pedicels, slightly constricted immediately below the slightly spreading and very narrow rim, finely veined, 6-6.5 mm. long and 5 mm. wide, with 3 or 4 deeply enclosed valves and an obscure disc. Seed (only one fertile one seen) blackish, obliquely subovate in outline, more or less truncate at one end, elsewhere with rounded margins, concavo-convex, with numerous excentric radial ridges and concentrically closely striolate, 2 mm. long and nearly as wide.

NORTHERN TERRITORY.—Maranboy Police Station, Jan. 1949, *Lullfitz;* wet alluvium of Lake Woods, 22 miles S. of Elliott, 19.viii.1948, *Perry* 1929; 16.7 miles N. of Helen Springs Station, 6.vii.1947, *Perry* 223.

Type.—Allen 636 from Newcastle Waters (NSW); Plate 35.

Only known from the specimens cited (map 30*C*). The type carries buds, flowers, and developing fruits, and is in much the same condition as Perry's specimens. The specimens collected by Lullfitz, examined through the courtesy of Mr. A. W. Jessep, show the complete series of developmental stages from bud to mature fruit, and made possible the extended description given here.

The operculum is sometimes much shorter than is usual among the "boxes" (sect. *Porantheroideae*), and Blakely has suggested a resemblance in the bud to the buds of *E. clavigera* and *E. papuana.* The frail, somewhat urceolate fruits with enclosed valves also resemble those of these species rather than of the *Porantheroideae,* but the bark, leaves, inflorescence, stamens, and seed are quite characteristic of the section, and bear a strong resemblance to those of *E. tectifica,* from which *E. cyanoclada* differs in that the intramarginal vein of the leaf is rather more distant from the margin, and in that the calyx-tube is produced in fruit well above the top of the capsule and there slightly but distinctly constricted. Immature fruits resemble those of some states of *E. microtheca,* with the domed apex of the ovary about level with the as yet expanded rim, and this led Blakely to associate the species with those with prominently exserted valves.

44. **Eucalyptus normantonensis** Maiden & Cambage in J. Roy. Soc. N.S.W. 52: 489 (1919)

E. bicolor A. Cunn. ex Maiden var. *xanthophylla* Blakely, Key Eucalypts 232 (1934).

E. largiflorens F. Muell. var. *xanthophylla* (Blakely) Cameron in Vict. Nat. 63: 42 (1946).

A mallee or small tree usually branched at the base, from less than 2 m. up to about 8 m. high; bark on the upper part smooth, brown, grey, or greenish, becoming rough, grey, fissured, and more or less flaky towards the lower part, particularly on the larger plants. Juvenile leaves linear-lanceolate, opposite for up to 8 pairs, glaucous, closely veined, sessile or nearly so on the sharply tetraquetrous stems, glabrous, about 3-5 cm. long and 0.3-0.4 cm. wide; intermediate leaves becoming larger and less narrowly lanceolate, distinctly petiolate, glaucous, up to about 10 cm. long and 2 cm. wide. Adult leaves alternate, prominently petiolate, shining green on both sides when fresh but duller and sometimes yellowish green when dry and then closely dotted, lanceolate or narrowly lanceolate, straight to somewhat falcate, acute or acuminate to more or less obtuse, decurrent to the petiole, mostly 6-11 cm. long and 0.7-1.5 cm. wide (5-14 times as long as wide), thick, with the midrib alone prominent; intramarginal vein close to the edge, but quite distinct from it; lateral veins in about 15-20 pairs at an angle of 25°-40° (mostly about 30°) with the midrib, but so fine and so immersed in the thick texture of the leaf as to be almost uncountable; petioles 0.7-1.1 cm. long. Inflorescences terminal and in the uppermost axils, paniculate but often reduced to 3-6-flowered umbels on peduncles about as long as the petiole. Buds on pedicels as long as or somewhat shorter than the calyx-tube and distinct from them, obovoid, about 3.5 mm. long and 2.5 mm. wide, the broadly conoid (sometimes apiculate) operculum one-half to two-thirds as long as the calyx-tube. Outer stamens without anthers; inner ones shorter; filaments with subulate tips; anthers very small, basifixed, orbicular, opening in oblique pores. Fruits shortly to prominently pedicellate (pedicels 1-3 mm. long), deeply cup-shaped, distinct from the pedicels, about 3-4 mm. long, about 3-4 mm. wide, slightly wrinkled, with a relatively broad rim about 0.4-0.5 mm. wide (including the narrow disc) and 3 deeply included (rarely nearly flush) valves.

NORTHERN TERRITORY.—Seven miles N. of Tennant Creek, truncated laterite soil with *E. brevifolia* and *Triodia* spp., 25.iv.1948, *Perry* 570; 4.3 miles N. of Tennant Creek, 30.vi.1947, *Perry* 145.

Types.—Of *E. normantonensis*: holotype, *Cambage* 3930 from Normanton, Queensland (NSW); figured in Maiden, Crit. Rev. *Eucalyptus* 5: Plate 187, Figures 7*a* and 7*b* (not 7*c* nor 7*d*), and Plate 36, Figure 1 of this paper. Paratype: Normanton, *Murchie* (NSW); figured in Maiden loc. cit., Figure 6. Topotypes: *Blake* 9069, 12477, 15122; see Plate 36, Figures 2 and 3.

Of *E. bicolor* var. *xanthophylla*: two syntypes—Camooweal, *S. A. White* and Barrow Creek, *S. A. White* (not found).

Widely spread in parts of the Northern Territory and Queensland between the 15- and 30-in. isohyets (map 30*D*).

In the original description, the fruits were described as being 4 mm. long and 3 mm. wide, with deeply included valves. This description was copied by Maiden (loc. cit., 156) but the figure of the fruits in Plate 187, Fig. 7*c*, allegedly drawn from the type, shows much larger fruits with more or less exserted valves. Blakely (loc. cit., 244) described the fruits as 4-6 mm. long and 3-5 mm. wide with protruding valves. Cambage's material carries buds in various stages and fruits, most of which are not quite mature. Associated with this material is a packet of pieces of a fruiting inflorescence marked in Cambage's hand : *Eucalyptus*/Normanton/Nov. 1918/. It will be noted that these pieces were collected some years after the type, but they are evidently the fruits figured by Maiden. They are also the fruits referred to by Blakely in a letter dated Oct. 7, 1935 as having been sent to Cambage by P. J. Ward, without leaves or buds and that "therefore they are open to doubt". Cambage, Maiden, and Blakely assumed that they represented mature fruits of *E. normantonensis*, but my copious material from Normanton, in all stages, shows that this is incorrect. The fruits on Cambage's specimens are fully developed and give an adequate idea of the perfectly mature fruits (see Plate 36). The fruits sent by Ward are very closely matched by those of *Blake* 15140 from Normanton, which appears to represent a form of *E. argillacea*.

E. bicolor A. Cunn ex Maiden var. *xanthophylla* Blakely (*E. largiflorens* F. Muell. var. *xanthophylla* (Blakely) Cameron) was founded on fruiting specimens that have not been located. So far as can be judged from the protologue, the specimens are conspecific with *E. normantonensis.*

E. normantonensis is well distinguished by its more or less mallee-like habit, the small buds, numerous staminodes, tiny anthers of the short, fertile stamens, and small fruits with enclosed valves. Apparently it is not closely allied to any of the other species discussed in this paper.

Series SIDEROPHLOIAE Blakely

45. **Eucalyptus jensenii** Maiden, Crit. Rev. *Eucalyptus* **6:** 255, Plate 228, Fig. 1 (1922) (*"Jenseni"*)

E. perplexa Maiden & Blakely in Maiden, Crit. Rev. *Eucalyptus* 8: 3, Plate 288, Fig. 4-5 (1929); *syn. nov.*

More or less deciduous tree up to 12 m. high, with blackish, rugged, deeply and coarsely furrowed bark, somewhat scaly-looking on small branches; twigs slender, terete or nearly so. Late juvenile and early intermediate leaves ovate or oblong-ovate, obtuse. Adult leaves ovate-lanceolate to lanceolate or oblong-lanceolate, 5-9 cm. long, 1-3 cm. wide, commonly 3-5 times as long as wide, more or less obtuse, concolorous, and dull, with about 12-17 pairs of slender, somewhat irregular and often very faint lateral veins at an angle of 30°-40° with the midrib; petioles 0.5-1.1 cm. long. Flowers in shortly pedunculate, 3-7-flowered, axillary umbels and also in short, terminal panicles; peduncles 4-6 mm. long, pedicels up to 2 mm. long or rudimentary. Buds obovoid-globular, about 3.5 mm. long and wide; operculum more or less hemispherical, about as long as the calyx-tube. Anthers basifixed, globose-ovoid, opening in circular pores or short slits. Fruit cup-shaped or hemispherical, shortly pedicellate, 3.5-5 mm. long, 3.5-5 mm. wide, with 3 almost flush to shortly exserted valves.

NORTHERN TERRITORY.—Twenty miles E. of "Limbunya", open forest community with *E. terminalis*, red lateritic soil, 28.vi.1949, *Perry* 2310; between Mary R. and Coirwong Ck., 13° 5′ S., 132° E., two small groups associated with *Eucalyptus polycarpa* and *E. grandifolia* on light grey soil, about 75 m., 29.ix.1946, *Blake* 17096.

Types.—Of *E. jensenii*: *Jensen* 372 from near Wandi (NSW); figured in Maiden, loc. cit., excluding Figure 1*f*.

Lectotype of *E. perplexa*: between Erskine Range and Mount Marmion, *W. V. Fitzgerald* (NSW); figured in Maiden, loc. cit., Plate 288, Figure 4.

Known from several localities in the Kimberley division of Western Australia and the northern part of the Northern Territory, but its occurrence appears to be very restricted at each of the rather widely scattered localities (map 27).

The type of *E. jensenii* consists of abundant material in bud, flowers, and young fruit, with some late juvenile and intermediate leaves. Jensen explicitly stated on his field label "no ripe fruits yet available. Bark, leaves flowers & young fruits sent"; Miss Flockton has written on the sheet "Sucker leaf & buds drawn 12.8.21" and "Anther drawn 8.5.22". Maiden, however, described and figured apparently mature fruits alleged to belong to this collection; I have not found the source of these fruits, but it is evident that they do not form part of *Jensen* 372.

Four collections were cited in the protologue of *E. perplexa* without mention of a type. It appears certain that all four collections were used in preparing the description; two were figured. Of the latter, Spencer's specimen from Roper River Crossing (Fig. 5) was stated to be "not quite so glaucous" as the others, and in the explanation to the plate it was remarked that the valves of the fruit were exserted. It appears that the authors thought that this specimen was less representative of the species than the others, and so it may be neglected when choosing a lectotype; the sheet is marked "Drawing made 3.3.26. M.F." in Miss Flockton's writing. According to the explanation on p. 67, Figure 4 was drawn from *Fitzgerald* 1082 from "Isdell River, near Mount Barnett Homestead". This locality appears on labels to two sheets under this number at Sydney; one of them was marked by Miss Flockton "Drawing made 2.3.26. M.F." and the other has a second label (field label) with the locality "Between Isdell & Barnett Rivers". These two sheets are evidently part of the same collection, but there is also a third sheet under this number with the locality "Barnett River". These sheets carry no juvenile leaves such as figured in 4*a* and nearly all the fruits are slightly smaller than those figured in 4*b*. The juvenile leaf and larger fruits are, however, present on the sheet from "Between Erskine Range and Mount Marmion" (the latter name misquoted "Mount Marrion" in the protologue) and this sheet is marked "Drawing made 3.3.26 M.F." by Miss Flockton. It would appear that some error crept into the explanation of the plate and that Figure 4 was really drawn from this collection, which should be selected as lectotype.

Judged only from Maiden's figures, *E. jensenii* and *E. perplexa* appear distinct from one another, owing to the narrower leaves of the fruiting specimens of the latter and the broader leaves of the flowering twigs of the former. The difference is emphasized by the extraneous fruits associated by Maiden with the type of *E. jensenii*. But the leaves on both Jensen's and Fitzgerald's specimens are much more variable than is suggested by these figures, and parts of each resemble one another very closely. My specimens cited above have leaves closely matching the figure of Jensen's specimens and fruits matching those on Fitzgerald's specimens, while Perry's specimens have rather larger fruits and both broad and narrow leaves. There seems no doubt that both names refer to one and the same species, which is distinguished by the following combination of characters: Bark of the characteristic "ironbark" type, terminal and also axillary inflorescences, broad juvenile and intermediate leaves, small anthers opening in lateral pores, and small, smooth, nearly hemispherical fruits with slightly included to slightly exserted valves. It is the only characteristic "ironbark" known from the Northern Territory or Western

Australia. Its closest allies are most likely to be found among the narrow-leaved ironbarks of northern Queensland (*E. staigeriana* F. Muell. ex F. M. Bail., *E. drepanophylla* F. Muell. ex Benth., *E. crebra* F. Muell., *E. whitei* Maiden, and *E. cullenii* Cambage), but all of these have longer and sometimes wider buds more or less tapering into longer pedicels and mostly longer and also wider fruits, while *E. whitei, E. crebra,* and *E. cullenii* have narrow juvenile leaves. *E. staigeriana* is less unlike *E. jensenii* than are the other species because of a general resemblance in foliage and the production of axillary as well as terminal panicles; its latitudinal range is also much the same, but it appears to be restricted to more or less hilly country in the eastern part of Cape York Peninsula.

46. **Eucalyptus pruinosa** Schau. in Walp. Repert. 2: 926 (1843); non Turcz. (1849), nec Behr ex Miq. *in syn.* (1856)

E. spodophylla F. Muell. Fragm. 2: 71 (1860), *nomen nudum.*

A small, scraggy tree with few crooked, spreading branches, with grey, fissured, often more or less flaky-looking bark up to the twigs, sometimes flowering as a shrub; younger parts pruinose; twigs angular to more or less terete. Leaves opposite, sessile, ovate or oblong, obtusely rounded to subacute, prominently cordate, very pruinose at first but becoming only subglaucous in old age, 4-12.5 cm. long and 3-9 cm. wide, 1-2.3 times as long as wide, with a double intramarginal vein (the outer one more or less contiguous to the margin and the inner one about 2-3 mm. distant) and about 9-12 pairs of lateral veins making an angle of 50°-60° with the midrib; intermediate leaves much larger on prominently tetraquetrous stems; juvenile leaves not cordate, somewhat cuneate at the base. Panicles terminal, more or less pyramidal, shorter than the leaves; umbels several-flowered; pedicels up to as long as the buds and fruits. Buds more or less pruinose, 8-10 mm. long, 3-4 mm. wide, not or scarcely ribbed, the acutely conical or more or less acuminate operculum as long as or nearly as long as the more or less pyriform calyx-tube. Anthers globular, basifixed, with distinct cells opening in short, broad slits or circular pores. Fruits cup-shaped, from 7 mm. long and 5 mm. wide up to 10 mm. long and 8 mm. wide, with 4 or 5 deltoid valves inserted shortly below the orifice and shortly protruding beyond the narrow, flattish rim.

NORTHERN TERRITORY.—Near Katherine, 14° 25′ S., 132° 19′ E., dominating an open scrub-grass community on shallow, hard, reddish soil, about 110 m., 13.x.1946, *Blake* 17220; 15 miles NW. of Limbunya Station, on skeletal soils and brown loam soils on dolerite, 30.vi.1949, *Perry* 2312.

QUEENSLAND.—Ten miles W. of "Westmorland", sandy soil, 2.vi.1948, *Perry* 1150.

Type.—Islands of the Gulf of Carpentaria, *Brown & Bauer* (W); figured in Maiden, Crit. Rev. *Eucalyptus* 2: Plate 54, Figure 5.

A species widely spread from north-western Western Australia across the Northern Territory to north-western Queensland, chiefly in the region between the 15- and 35-in. isohyets, and commonly known as "silver box" (map 29*A*).

The species is readily distinguished from all others known from the Northern Territory by the more or less pruinose, opposite, broad, cordate, sessile leaves associated with short, terminal panicles and rough, grey bark. It is closely allied to *E. melanophloia* F. Muell., a species widely spread in Queensland and New South Wales (map 29*B*), which has a harder, blackish, rugged bark, smaller leaves on the average, rather shorter buds, and more rounded fruits that are usually smaller and usually with included valves.

To the east of its range, *E. pruinosa* is represented by the closely similar *E. shirleyi* Maiden (map 29*C*). The two species resemble one another in habit and in the general characters of foliage, buds, and anthers, but the trees of *E. shirleyi* are sometimes even more crooked, the bark is of the characteristic "ironbark" type as in *E. melanophloia*, the juvenile leaves have a greater tendency to be cordate, the pedicels are short or rudimentary, the calyx-tube in bud, flower, and fruit is more or less distinctly 3- or 4-ribbed, the operculum is much shorter than the calyx-tube, the fruit tends to be truncately obovate in outline and somewhat larger, and the valves are deeply enclosed. The type is *Bancroft* 180 from Stannary Hills (NSW, BRI); the material at Brisbane is in fruit only, but the material at Sydney (which I have not seen) appears to carry young buds from which Maiden and Blakely described the anthers as being versatile, so that Blakely associated the species with *E. gamophylla* F. Muell., *E. argillacea* W. V. Fitzg., and *E. intertexta* R. T. Baker. There are several specimens at Brisbane agreeing well with the type except that there is some variation in the size of the fruits and the prominence of the ribs. Of these only Kenny's specimens from Herberton (not far from the type locality) and *Blake* 14845 from Ravenswood carry mature buds and expanded flowers with mature fruits; the latter collection also is the only one showing juvenile leaves, intermediate leaves, or bark. From these two collections, it is evident that mature anthers closely resemble those of *E. pruinosa*.

47. **Eucalyptus crebra** F. Muell. in J. Linn. Soc. (Bot.) 3: 87 (1859)

Metrosideros salicifolia α Soland. ex Gaertn. Fruct. 1: 171, t. 34, fig. 3 (*left-hand part*) (1788); non *Eucalyptus salicifolia* Cav. (1797).

Eucalyptus gracilis Sieb. ex Benth. Fl. Aust. 3: 222 (1867) *nomen nudum;* non F. Muell. (1855).

Tree to 30 m. high with persistent, hard, thick, rough, very deeply furrowed, very dark grey to black bark up to the small branches; twigs slender. Juvenile leaves opposite for few (4 or 5, according to Maiden and to Blakely) pairs, shortly petiolate, narrowly linear to narrowly lanceolate-linear, glabrous. Intermediate leaves lanceolate-linear to narrowly lanceolate, mostly narrower than the adult ones. Adult leaves dull or more or less glaucous, especially when dry, alternate, prominently petiolate, lanceolate and more or less falcate, narrowly obtuse to more or less acute or acutely acuminate, mostly 8-15 cm. long and 0.8-1.8 cm.

wide, mostly 7-11 times as long as wide, with the intramarginal vein very close to the margin (rarely as much as 0.7 mm. distant from it), and about 20-27 pairs of fine primary veins at an angle of 30°-40° with the midrib. Panicles terminal, sometimes leafy at the base, shorter than the leaves; umbels 3-7-flowered on slender peduncles; pedicels slender, widened upwards, 2-5 mm. long. Buds obovoid to fusiform, obtuse or more or less acuminate, rather gradually narrowed to the pedicel, 4-6 mm. long, 3-3.5 mm. wide; operculum from half as long to as long as the calyx-tube, more or less hemispherical to conoid or somewhat acuminate. Stamens all perfect; anthers nearly globular to somewhat oblong, basifixed, with a small, terminal gland and parallel cells opening throughout their length in broad slits. Fruits pedicellate, cup-shaped to truncate-ovoid, 4-6 mm. long, 4-5 mm. wide, with a narrow rim that is sometimes slightly incurved and an obscure disc; valves 3 or 4, from slightly included to slightly exserted.

The above description refers to the common state of the species and excludes a form from inland south-east Queensland at present referred to it but with markedly smaller buds and fruits and smaller, more glaucous leaves. The anthers vary in length from 0.25 mm. to 0.4 mm., and are commonly about 0.35 mm.; Maiden and Blakely appear to have regarded the smaller anthers as characteristic for the species and have attempted to use it as a character distinguishing *E. crebra* from *E. drepanophylla.*

Distribution.—Eastern Queensland and eastern New South Wales.

Types.—Of *E. crebra*: "Burdekin", 10.xi. 1856, *F. Mueller* (MEL, BRI); (at this date Mueller was away from the Burdekin River itself, and was WNW. to W. of the site of the present town of Blair Athol, on the northern and western approaches to the Drummond Range).

Of *Metrosideros salicifolia*: Thirsty Sound, *Banks and Solander;* duplicate in NSW; fruit and sterile seeds figured by Gaertner (loc. cit.) flowering and fruiting specimen figured by Britten, Bot. Cook's Voy. 2: Plate 117, under the name of *E. terminalis* F. Muell.

Of *E. gracilis*: *Sieber Pl. Exs.* 476 (not seen).

In the protologue, Mueller stated that *Eucalyptus crebra* occurred frequently between Newcastle Range and Moreton Bay, and that its abundance suggested the specific epithet. Apparently only one specimen from this region collected and labelled by Mueller has been preserved; the label reads: Eucalyptus crebra/Ironbark tree of Nov 10/Burdekin/. Reference to Gregory's journal shows that on this date the party was WNW. to W. of the site of the present town of Blair Athol, on the northern and north-western approaches to the Drummond Range; this is in the watershed of the Burdekin River, but a long way distant from the river itself. This specimen must be accepted as the type; it is in fruit and young bud and is very like the specimens usually referred to the species. Two other collections were found in the Melbourne Herbarium that had been collected in 1856 by Mueller and labelled by him *Eucalyptus crebra.* One of these, from "scrub country between the Albert & Flinders" bears the later determination in Mueller's hand: "E. bicolor All. Cunn. ex Black", and is a specimen of *E. normantonensis* Maiden and Cambage; the other, from "Between the Flinders and Lynd Rivers", in fruit and very young bud, has not yet been determined, but it appears to represent a species distinct from any of those discussed in this paper.

Blakely (loc. cit., pp. 59, 248, 319, etc.) used the name *E. racemosa* Cav. for this species. At Melbourne, there is a small, unlabelled specimen in young bud in a packet marked in Mueller's hand "E collectione Cavanillesii dedit Colmeiro" (from the collection of Cavanilles; Colmeiro gave it). This specimen agrees well with Cavanilles' description, and is accepted here as being portion of the type. The inflorescence is too immature to allow of certain determination, but the venation of the leaves shows that it belongs to a species quite different from *E. crebra,* but apparently allied to such species as *E. micrantha* DC., *E. radiata* Sieb., or *E. amygdalina* Labill.

Gaertner described and figured *Metrosideros salicifolia* from specimens collected by Banks and Solander and described in MS. by Solander. Gaertner's figure and description refer to fruits and seeds only; two forms were recognized and distinguished by the Greek letters α and β. Solander's MS. account and a plate prepared in 1778 by F. P. Nodder from a specimen from Thirsty Sound were published by Britten in Illustr. Bot. Captain Cook's Voy. 2: 39 and Plate 117 (1901) under the name *Eucalyptus terminalis* F. Muell.; Solander's description evidently refers to two species at least, one with a thick, cracky bark and another with a smooth, deciduous bark. From Gaertner's work, it would appear that Solander distinguished at least five forms for which he used the inclusive name of *Metrosideros salicifolia;* Gaertner (loc. cit., 174, t. 35) based his *Leptospermum umbellatum* on *"Metrosideros salicifolia* V. SOLAND. *mss.*", which is usually (although the description and figure apply much better to *E. exserta* F. Muell.) treated as a synonym of *Eucalyptus tereticornis* Sm. (*E. umbellata* (Gaertn.) Domin (1928), non Dum.-Cours. (1814)). In the Sydney Herbarium there is a sheet from Banks and Solander's collections carrying pieces of two species that are rather similar in foliage; one of these species is represented in leaf only, but the pieces of the other species carry also buds, flowers, and immature fruits and correspond to Nodder's plate. Nodder's drawing, the fertile material in herb. Sydney, and *Metrosideros salicifolia* α are all to be referred to *E. crebra,* which would be Solander's tree with thick, cracky bark. The other leaves at Sydney belong to *E. papuana;* the smooth bark and the other locality quoted by Britten, Lizard Island, could refer to this (Banks and Solander's specimens of *E. tereticornis* were collected at Bay of Inlets, according to Bentham, Fl. Aust. 3: 242). *Metrosideros salicifolia* β remains a puzzle; the fruits and seeds closely resemble those of *E. microcorys* F. Muell., but there appears to be no record of its occurrence anywhere near any locality visited by Banks and Solander.

Hence *Metrosideros salicifolia* Soland. ex Gaertn. refers chiefly to *Eucalyptus crebra* F. Muell. *Eucalyptus salicifolia* Cav. (loc. cit.) appears to have been described independently of Solander and Gaertner, so far as can be judged from the copy of the original description quoted by Maiden (op. cit. **1**: 235 (1907)), for the original is not available in Australia. Also, from Maiden's quotation (op. cit. **3**: 50) of the description, Cavanilles has queried whether his *E. platypodos* might not be "*Metrosideros salicifolia* Gaertneri vol. I Tab. 34 fig. 3a?" Blakely therefore has erred in quoting this name as *Eucalyptus salicifolia* (Sol.) Cav., and both he and Maiden have erred further in associating Gaertner's name (founded on a tropical Queensland plant) with a Tasmanian plant, *E. amygdalina* Labill. The existence of the name *Eucalyptus salicifolia* Cav. prevents the use of Solander's epithet under *Eucalyptus*. So far as Cavanilles' description is concerned, it seems to exclude *E. amygdalina;* the asymmetric leaves very oblique at the base, ascending nerves, and 7-10-flowered axillary umbels do not well accord and may apply to *E. obliqua* L'Hérit. The name *E. amygdalina* Labill. should remain in use for the Tasmanian tree.

In Vict. Nat. **63**: 40 (1946), A. K. Cameron rejected Blakely's use of the name *E. salicifolia* instead of *E. amygdalina* on the grounds that *Metrosideros salicifolia* was founded entirely on plants collected by Banks and Solander who could not possibly have collected a Tasmanian endemic, and that *E. salicifolia* Cav. is of uncertain application but is not "synonymous" with *Metrosideros salicifolia.* Cameron has adduced sufficient evidence (much the same as that given above) to show that *E. salicifolia* was not founded on *M. salicifolia,* but as he remained doubtful of the application of each of these names, he was scarcely justified in stating that they were not synonymous, i.e. that they did not apply to one and the same species. He has given no evidence for rejecting Blakely's use of Cavanilles' name for the Tasmanian plant — only evidence that Blakely wrongly quoted it on the erroneous assumption that it was based on Solander's name.

Franco (*Bol. Soc. Brot.* II **23**: 164-5 (1949)) also pointed out that *E. salicifolia* Cav. was not based on *Metrosideros salicifolia* Gaertn. He thought it possible that both names could refer to *E. amygdalina,* but he preferred to use the last-mentioned name because its correct application was quite clear.

The name *Eucalyptus gracilis* Sieb. appeared on the label to Sieber's Pl. Exs. n. 476. This name was mentioned incidentally by Bentham when remarking that the specimen appeared to represent a form of *E. crebra.* Maiden (Crit. Rev. *Eucalyptus* **2**: 64) stated that he saw specimens under this number at Kew and Vienna and that he agreed with Bentham; for this reason the name is cited above. Maiden (loc. cit.) listed *E. haemastoma* DC. non Smith, *E. terminalis* Britten non F. Muell., and *E. angustifolia*

Woolls as synonyms of *E. crebra.* The first two of these are misapplications of earlier names, and the third is a *nomen nudum* published without any reference to specimens.

48. **Eucalyptus drepanophylla** F. Muell. ex Benth. Fl. Aust. 3: 221 (1867)

?*E. crebra* F. Muell. var. *macrocarpa* Domin in Bibl. Bot. 89: 465 (1928).

?*E. racemosa* Cav. var. *macrocarpa* (Domin) Blakely, Key Eucalypts 249 (1934).

A tree more or less resembling *E. crebra* in bark and habit, but never so tall. It differs from this chiefly in the ovate intermediate leaves (up to 10 × 5 cm. in the few specimens seen); in that the adult leaves are, on the whole, rather wider, mostly 5.5-8 times as long as wide, with the intramarginal vein more distant (0.6-1, though usually at least 0.8 mm.) from the margin and the lateral veins at an angle of usually 40°-50° with the midrib; the larger buds 7-8 mm. long and 3-4 mm. wide more gradually narrowed to the coarser pedicels; and the sometimes slightly larger fruit 5-7 mm. long and 5-6 mm. wide with more regularly exserted valves.

Distribution.—Queensland, chiefly north-eastern Queensland.

Types.—Of *E. drepanophylla*: four syntypes, of which Maiden has selected *Dallachy's* specimen from Edgecumbe Bay (NSW, BRI), figured in Crit. Rev. *Eucalyptus* 5: Plate 200, Figure 1.

Of *E. crebra* var. *macrocarpa*: Townsville, *Domin* (herb. Domin); not seen.

Of the specimens cited by Bentham under this species, I have seen all those written up by Mueller, namely those collected by Fitzalan, Dallachy, and Bowman. Maiden (loc. cit., 262) very arbitrarily chose Dallachy's specimen from Edgecumbe Bay as the type (lectotype); a second label with this specimen was written up by Mueller as Port Denison, and this is the locality cited by Bentham. Of the other specimens quoted by Bentham, *Brown* 4730 from Keppel Bay appears to be rather *E. crebra,* at least as to the specimen at Melbourne. I have not seen Brown's specimens from Shoalwater Bay nor Cunningham's specimens; according to Maiden in Ewart & Davies, Fl. North. Territ. 308 (1917) and in Crit. Rev. *Eucalyptus* 4: 207 (1919), Cunningham's specimens from the north-west coast are of *E. spenceriana* (*E. tectifica* F. Muell.). Bentham's description of the fruits has certainly been drawn from specimens of another species; could it have been drawn from Cunningham's east coast plants and could these have been *E. leptophleba?*

The earlier confusion between *E. drepanophylla* and *E. leptophleba* has been discussed and unravelled by Maiden (op. cit. 1: 332-4 (1908) and 5: 261-7, Plates 200-1 (1921)). As he pointed out (op. cit. 5: 263) *E. drepanophylla* and *E. crebra* are often difficult to distinguish; on the whole, *E. drepanophylla* has broader leaves, decidedly so in the juvenile stages, less constantly so in the adult stage (it is almost impossible to distinguish between the leaves of the type specimens of the two species). The buds and flowers of *E. drepanophylla* are rather larger with coarser pedicels, but I do not find the difference in the anthers stressed by Maiden.

Flower-bearing specimens with leaves and fruits matching the type of *E. crebra* (*White* 7006, *Blake* 15707, 13146) have anthers precisely similar to those of the syntypes of *E. drepanophylla*; Maiden's figure of the anthers from specimens from New South Wales (op. cit. 2: Plate 53, Fig. 5*b*) does not quite agree with Queensland specimens. It is possible that *E. crebra* var. *macrocarpa* also refers to *E. drepanophylla,* which is fairly common in the neighbourhood of Townsville, Domin's type locality, but I have not seen Domin's specimen. *E. hemiphloia* F. Muell. ex Benth. var. (?) *parviflora* Benth. Fl. Aust. 3: 217 (1867), based on specimens of an "ironbark" collected by Fitzalan on Mt. Elliott, is also probably the same.

E. decepta Blakely, Key Eucalypts 249 (1934) also appears to be conspecific. No specimens are cited in the protologue, only a number of localities from south-eastern Queensland and north-eastern New South Wales. There is a reference to a figure of a fruit in Maiden Crit. Rev. *Eucalyptus* 2: Plate 57, Figure 13, drawn from a specimen from Casino, N.S.W., collected by W. P. Pope. Blakely remarked that the species had been confused with *E. paniculata* Sm., *E. racemosa* (i.e. *E. crebra*), and the narrow-leaved form of *E. siderophloia* Benth. I have examined only the material at Brisbane. There is at least one collection that was examined by Blakely prior to the publication of the name, the locality of which is cited in the protologue, and several specimens determined by him since the publication. The form is quite common in the neighbourhood of Brisbane, and I have been able to study it in some detail. The trees in southern Queensland have usually been referred to *E. paniculata;* fruiting specimens of the two forms are often extraordinarily alike except for the strongly discolorous leaves of *E. paniculata*, but the anthers are very different. Blakely cited several Queensland localities for *E. paniculata* on p. 257, some of which are the same as those cited for *E. decepta;* it seems likely that these were quoted in error. Both Mr. C. T. White and myself were convinced that true *E. paniculata* has not yet been found in Queensland.

Apparently owing to the long-standing confusion of specimens from New South Wales and southern Queensland with *E. paniculata* when in fruit and with *E. crebra* when in flower, Blakely failed to compare them with *E. drepanophylla.* The southern plants tend to have a rather acutely conical and nearly or quite smooth operculum compared with the rather blunt and more or less wrinkled operculum usually found on northern plants, but there are specimens with intermediate characters uncorrelated with distribution. Throughout the range of the species in Queensland (at least) the trees are much alike in habit, and no difference has yet been observed in the timber. The specimens examined indicate a continuous area of distribution from the Atherton Tableland in the north to north-eastern New South Wales, in coastal and subcoastal districts. (Since the above was written, a study of the trees in the type localities of *E. drepanophylla, E. crebra* var. *macrocarpa,* and *E. hemiphloia* (?) var.

parviflora has convinced me that these names and *E. decepta* refer to one species, of which the correct name is *E. drepanophylla.*)

Series SUBULATAE Blakely

49. **Eucalyptus umbrawarrensis** Maiden, Crit. Rev. *Eucalyptus* **6**: 257, Plate 228, Fig. 2 (1922)

Shrubby or straggly tree up to 9 m. high with smooth and white, deciduous bark and slender, angular twigs. Intermediate leaves nearly orbicular to ovate, green and more or less shining, prominently petiolate, up to 8 × 5 cm. Adult leaves green or glaucous, alternate, petiolate, narrowly lanceolate, 6-10 cm. long, 1-1.6 cm. wide, 5-10 times as long as wide, with about 15-24 pairs of very fine and mostly indistinct lateral veins at an angle of 30°-40° (or up to 50°) with the midrib; intramarginal vein very close to the margin; petioles 8-12 mm. long. Inflorescence of axillary umbels; peduncles about 5-7 mm. long; pedicels 2-2.5 mm. long. Buds turbinate-obovoid, about 3 mm. long and 2.5 mm. wide, narrowed to the pedicel; operculum nearly hemispherical, somewhat apiculate, two-thirds as long as the calyx-tube and somewhat narrower than it. Anthers basifixed, reniform, with contiguous cells opening laterally nearly throughout their length in broad slits or elliptic pores; gland small, terminal; filaments attenuate in their upper part. Fruits turbinate, tapering to their pedicels, 3-4 mm. long and 3-3.7 mm. wide, irregularly wrinkled (lacunose) with a thin rim, a narrow descending disc, and 3 or 4 short and broad, more or less exserted valves.

NORTHERN TERRITORY.—Forty-four miles from Katherine on Willeroo Road, top of steep breakaway, 3.vi.1949, *Perry* 1999; N. of Nutwood Downs homestead, on lateritic tableland, 168 m., locally dominant, 1.v.1947, *Blake* 17583.

Type.—Jensen 412 from Umbrawarra (NSW); figured in Maiden (loc. cit.).

This species is known only from the three collections cited above, and appears to be very rare with a strongly discontinuous distribution (map 23*B*).

The type material consists of several adult leafy twigs with inflorescences in extremely young bud which are quite pruinose; loose, well-developed buds; an old flower; and some mature fruits. The other specimens agree as to fruit and the shape, size, and venation of the leaves but are not pruinose. The only anthers I have seen are those mentioned in the protologue. The figure (2*c*) shows the pores in the upper part only of the cell, and this is as much as can be seen of them from this view of the anther; actually the pores extend almost to the base of each cell.

Intermediate leaves have not previously been described; juvenile leaves are unknown.

This species is best distinguished by the following combination of characters: smooth, white bark; narrow leaves with very fine and indistinct veins, which are relatively few in number and at a rather acute angle to the midrib; intramarginal vein very close to the margin; axillary umbels with short pedicels; small buds with the operculum shorter and rather narrower than the calyx-tube; reniform anthers on attenuated filaments and opening in large lateral pores; and small fruits with narrow rim and disc and short, more or less exserted valves.

50. **Eucalyptus pachyphylla** F. Muell. in J. Linn. Soc. (Bot.) 3: 98 (1859); non A. Cunn, ex Hook. f. in J. Linn. Soc. (Bot.) 3: 98 (1859) *in nota, nomen* et ex Maiden, Crit. Rev. *Eucalyptus* 1: 101, 103, *in syn.* (1904).

E. pyriformis Turcz. var. *minor* Maiden, Crit. Rev. *Eucalyptus* 2: 230 (1912).

E. pachyphylla F. Muell. var. *pedicellata* Maiden in Proc. Roy. Soc. N.S.W. 52: 508 (1919), *nomen nudum.*

A characteristic mallee about 1.5 m. high with numerous slender, smooth, white stems and reddish twigs and petioles. Leaves on rather long petioles (about 1.5-2 cm. long), ovate to broadly lanceolate, acute or acutely acuminate and sometimes curved in the upper part, rounded but sometimes with very unequal sides at the base, about 6-10.5 cm. long and 2.2-5 cm. wide, 2-3 times as long as wide, thick and more or less glaucous, the 12-15 pairs of lateral veins very faint at an angle of 40°-50° with the midrib. Flowers axillary, solitary or in 2- or 3-flowered, shortly pedunculate umbels; pedicels very short or up to 6 mm. long; buds red, ovoid-acuminate, with about 6 prominent ribs and sometimes with fainter ones between, 1.8-2.5 cm. long and 1.3-2 cm. wide, the calyx-tube broader than long; operculum widest shortly above the base, twice as long as the calyx-tube. Stamens very numerous, cream or yellow, the filaments with very slender, subulate tips; anthers attached at or near the base, nearly as broad as long, and more or less emarginate at top and bottom, with distinct, nearly parallel cells opening in wide lateral slits. Fruits shortly pedicellate, oblate, with a short, nearly horizontal calyx-tube with 3-6 prominent ribs; a thick disc occupying the greater part of the height of the fruit, slightly tapering upwards but more or less expanded at the broad top, and 3 or 4 stout, exserted, incurved valves, in all 1.3-1.7 cm. long and 1.8-3 cm. wide.

NORTHERN TERRITORY.—20.2 miles N. of Tennant Creek, 30.vi.1947, *Perry* 159; neighbourhood of "Frewena", about 19° 30′ S., 135° 30′ E., low, open desert scrub with *Plectrachne schinzii*, hard, red soil, about 225 m., widely spread, 16.vi.1946, *Blake* 15984; 28 miles ESE. of "Frewena", red, lateritic soil with *E. brevifolia*, 28.iv.1948, *Perry* 653.

Widely spread and locally dominant in the desert scrub in the region of the 15-in. isohyet, from near the Western Australian border to just across the Queensland border (map 23*C*).

Types.—Of *E. pachyphylla*: Hooker Creek, *F. Mueller* (MEL); figured in Maiden, Crit. Rev. *Eucalyptus* 5: Plate 171, Figure 1.

Of *E. pachyphylla* var. *pedicellata*: plate labelled *E. pachyphylla* in F. Muell. Eucalyptogr. dec. 1.

Of *E. pyriformis* var. *minor*: based nomenclaturally on *E. pachyphylla* F. Muell.

Juvenile leaves have not been described. According to a photograph (AFSC) of seedlings raised by Jacobs in Canberra (S.664), the cotyledons are very deeply bilobed, almost bipartite, with narrowly oblanceolate lobes, and the juvenile leaves are opposite for at least six pairs, oblanceolate or lanceolate to ovate, obtuse, with long and slender petioles.

E. pachyphylla is allied to the Western Australian *E. pyriformis* Turcz., but this has relatively long peduncles and pedicels, much larger buds and fruits with the calyx-tube about as long as broad, and the disc gradually sloping upward to a thin, not expanded top. *E. sessilis* (Maiden) Blakely, based on specimens from the Macdonnell Ranges, appears to differ only in having very rudimentary peduncles and pedicels and 3-7-flowered umbels.

The mallee habit with thick, glaucous leaves and red twigs and petioles, the rather large, ribbed buds in 1-3-flowered axillary inflorescences with short peduncles and pedicels, the fairly large fruits with a short, broad, ribbed calyx-tube, tall and stout disc, and stout, exserted valves together make the species an easy one to recognize.

VII. SUMMARY OF NOMENCLATURAL CHANGES PROPOSED IN THIS PAPER

It has been shown in the earlier part of this paper that some names have been wrongly applied, while many others are unnecessary because they appear to refer to previously named units and are therefore synonyms of other names. The correlation of these names is summarized in the following tables. For convenience of reference, the names accepted in Blakely's "A Key to the Eucalypts" are arranged in alphabetical order in the column to the left; the legitimate (correct) names as interpreted in this paper are in the right-hand column. Although these misapplications are here listed from Blakely, it must be stressed that in nearly every case Blakely followed Maiden's interpretations, and that some of the errors are of very long standing; the history of each misapplication has been discussed in detail under the species concerned. No author's name follows a misapplied name. The treatment of synonyms is partly an expression of taxonomic opinion, and so a partial reflection of the state of knowledge of the groups. The names treated as synonyms for the first time in this paper are marked with an asterisk.

TABLE 1

MISAPPLIED NAMES

Name Used by Blakely	Legitimate Name of Species
E. clavigera	*E. confertiflora* F. Muell. (The name *E. clavigera* was correctly applied to very few specimens)
E. foelscheana	*E. foelscheana* F. Muell. + *E. porrecta* S. T. Blake; Jacobs's account refers to the latter species except for the copy of the original description
E. polycarpa	*E. terminalis* F. Muell.
E. racemosa	*E. crebra* F. Muell.
E. salicifolia	*E. amygdalina* Labill.
E. terminalis	*E. polycarpa* F. Muell.

In addition to the above, the following legitimate names were treated as synonyms as the result of misapplication: *E. bigalerita* F. Muell., *E. brevifolia* F. Muell., and *E. confertiflora* F. Muell.

TABLE 2

SYNONYMS

Name Used by Blakely	Legitimate Name
E. alba Reinw. ex Bl. var. *australasica* Blakely & Jacobs*	*E. alba* Reinw. ex Bl.
E. arenaria Blakely*	*E. dichromophloia* F. Muell.
E. bicolor A. Cunn. var. *xanthophylla* Blakely*	*E. normantonensis* Maiden & Cambage
E. camaldulensis Dehn. varr.	*E. camaldulensis* Dehn.
E. clavigera A. Cunn. var. *diffusa* Blakely & Jacobs*	*E. confertiflora* F. Muell.
E. clavigera A. Cunn. var. *gilbertensis* Maiden & Blakely*	*E. gilbertensis* (Maiden & Blakely) S. T. Blake
E. coolabah Blakely & Jacobs*	*E. microtheca* F. Muell.
E. coolabah Blakely & Jacobs var. *arida* Blakely*	*E. microtheca* F. Muell.
E. erythrophloia Blakely*	*E. dichromophloia* F. Muell.
E. hillii Maiden*	*E. oligantha* Schau.
E. hillii Maiden var. *alleniana* Blakely & Jacobs*	*E. oligantha* Schau.
E. leiophloia Blakely & Jacobs*	*E. foelscheana* F. Muell.
E. leiophloia Blakely & Jacobs var. *lepidophloia* Blakely & Jacobs*	*E. foelscheana* F. Muell.
E. leucophylla Domin*	*E. argillacea* W. V. Fitzg.
E. macropoda Blakely*	*E. terminalis* F. Muell.
E. microtheca F. Muell var. *cymbaliformis* Blakely & Jacobs*	*E. microtheca* F. Muell.
E. niphophloia Blakely & Jacobs*	*E. dichromophloia* F. Muell.
E. pallidifolia F. Muell.*	*E. brevifolia* F. Muell.
E. papuana F. Muell. var. *aparrerinja* Blakely (invalid name)	*E. papuana* F. Muell.
E. pastoralis S. Moore*	*E. bigalerita* F. Muell.
E. perfoliata R. Br. ex Benth. non Desf.*	*E. zygophylla* Blakely
E. perplexa Maiden & Blakely*	*E. jensenii* Maiden

TABLE 2 (*Continued*)

Name Used by Blakely	Legitimate Name
E. platyphylla F. Muell.	*E. alba* Reinw. ex Bl.
E. platyphylla F. Muell. var. *tintinnans* Blakely & Jacobs*	*E. alba* Reinw. ex Bl.
E. polycarpa F. Muell. var. *oligocarpa* Blakely & Jacobs*	*E. dichromophloia* F. Muell.
E. pyrophora Benth.	*E. terminalis* F. Muell.
E. spenceriana Maiden*	*E. tectifica* F. Muell.
E. tropica Cambage ex Maiden*	*E. argillacea* F. Muell.

VIII. KEYS TO THE SPECIES

In the following pages, three keys are presented for the identification of all species known to be indigenous to that part of the Northern Territory north of 20° S. lat. Species discussed in the earlier part of this paper that are not definitely known from this area are excluded. All keys are strictly dichotomous.

The first key is intended as a guide to the identification of living plants in the field, so that the characters used are those most readily observable under these conditions. Small or low-branched plants are characteristic of many species and on these some details of leaves and inflorescence (when present) are readily observed. The fruits remain on the tree for long periods in many species; they eventually fall, each on its pedicel, and these fallen fruits can usually be found beneath the trees. Some measuring instrument graduated in millimetres is the only equipment necessary. Characters of the juvenile and intermediate leaves have been rarely used and little provision has been made for trees with a predominance of reversion shoots and none for hybrids. Some discretion may therefore be required in using the key, but isolated plants of any species are rarely found so that several individuals are usually available for examination.

Two keys are provided for the determination of hand specimens or material in the herbarium. One is based on specimens in bud and flower with or without fruit and the other on specimens with fruit only. For the key for flowering specimens, some knowledge of the general nature of the inflorescence is desirable, but the other key can be used with loose fruits provided that they are fully formed and not too much weathered. No key can be used with developing fruit, because in many species very immature fruits are quite unlike the mature fruits and quite unlike the calyx-tube of the flower. Fertile seeds and juvenile leaves are so often unavailable that no use of them has been made in the keys.

A binocular microscope is useful for examining anthers, but it is by no means essential to the use of the key, in which the finer details of structure are not considered. Some instrument for measuring the angles of veins is required, such as a transparent protractor.

Every effort has been made to make each contrasting pair of paragraphs appear as distinct as possible from neighbouring paragraphs; one result of this is that any paragraph may not begin with the most distinctive character and it is important that each paragraph of a contrasting pair should be considered in full.

The field characters of the four species unknown to me in the living state have been taken from published and unpublished notes of other collectors; these species are *E. abbreviata, E. cliftoniana, E. nesophila,* and *E. brachyandra.*

KEY BASED ON CHARACTERS OBSERVABLE IN THE FIELD

1. Mallees; shrubs with several slender stems:

Leaves whitish with reddish petioles and midribs; buds and fruits prominently many-ribbed, at least 15 mm. long and wide .. .. 50. *E. pachyphylla*

Leaves green or somewhat whitish, but with pale-coloured petioles and midribs; buds and fruits with no more than 4 ribs, usually very much smaller:

Fruits with included valves 3-12 × 3-6 mm.; buds 3.5-5 × 2.5-4 mm.; adult leaves shining green, narrow to very narrow (6-15 mm. wide and 5-15 times as long as wide):

Fruits 8-12 × 5-6 mm., usually with 4 small teeth at or below the rim; buds 4-angled with 4 small teeth, 4-5 × 3-4 mm.; adult leaves partly opposite; juvenile and intermediate leaves sometimes connate .. .. .. 1. *E. odontocarpa*

Fruits 3-4 × 3-4 mm.; buds about 3.5 × 2.5 mm.; no angles or teeth; leaves never connate, the intermediate and adult ones alternate 44. *E. normantonensis*

Fruits with exserted valves or plants otherwise different from the above .. .. Stunted states of tree species

1. Trees with a single trunk, sometimes divided at or close to the base:

2. Trees with rough bark persistent up to the small branches and furrowed, flaky, scaly, or stringy; inflorescence chiefly axillary in *E. tetrodonta*, chiefly terminal in all others:

3. Bark grey or yellowish grey to dark grey or black, nowhere rusty or reddish:

4. Trees (usually small) with more or less wide-spreading branches, with broad, stiff, sessile or subsessile, opposite leaves:

Twigs (at least) ashy-grey or whitish, glabrous or nearly so:

Leaves also more or less pruinose; buds and fruits pedicellate, up to 10 mm. long, the latter with exserted valves .. .. 46. *E. pruinosa*

Leaves more or less pale green; buds and fruits nearly sessile, more than 10 mm. long, the latter with included valves .. .. 14. *E. abbreviata*

Twigs rusty or reddish or purplish, often hairy:

Twigs and at least some of the leaves rusty with a powdery indumentum easily rubbed off; fruit longer than wide .. .. 13. *E. ferruginea*

Twigs and sometimes the leaves with short, stiff, purplish hairs but no powdery indumentum; fruits about as wide as long .. .. .. 12. *E. setosa*

4. Trees of various habit with prominently petiolate, often more or less pendulous leaves on usually slender twigs:

Bark very hard, very rugged, deeply furrowed, dark grey to blackish (ironbark) .. .. 45. *E. jensenii*

Bark not so hard, often soft and brittle or strongly fibrous or flaky to scaly, not blackish except as the result of fire:

Bark with long fibres, more or less longitudinally but not transversely furrowed, neither flaky nor scaly:

Leaves more than 10 cm. long, prominently falcate, hanging vertically; juvenile and intermediate leaves glabrous; fruit 4-toothed . 2. *E. tetrodonta*

Leaves 6-9 cm. long, straight or slightly falcate, more or less horizontal; juvenile and intermediate leaves hairy on the lower surface; fruits not toothed .. .. 24. *E. jacobsiana*

Bark with short, sometimes interlocked fibres or not fibrous, sometimes brittle, variously scaly or flaky or tessellated:

Bark predominantly rather coarsely tessellately flaky with both vertical and horizontal furrows; fruits with deeply enclosed valves, widest at or below the middle ("bloodwoods"):

Leaves about the same colour on both sides; fruits about as wide as long .. .. 21. *E. porrecta*

Leaves distinctly paler on the lower surface; fruits distinctly longer than wide:

Fruits with 8 or more prominent, vertical ridges; leaves often very large, up to 35 cm. long .. .. 23. *E. ptychocarpa*

Fruit not ridged; leaves commonly not more than 15 cm. long:

Fruits 10 mm. or more wide, densely scurfy before weathering; no peltate leaves at any stage .. .. 16. *E. polycarpa*

Fruits 7-8 mm. wide, somewhat pustular but not scurfy; some juvenile or intermediate leaves peltate .. .. 25. *E. nesophila*

Bark irregularly vertically furrowed to irregularly scaly with more or less interlocked fibres, not tessellated; fruits often with flush to exserted valves, usually widest above the middle or cylindrical ("boxes"):

Leaves mostly broadly ovate to deltoid or more or less oblong and then very obtuse (1-3 times as long as wide with 12-20 pairs of lateral veins):

Leaves 5-8 cm. long, discolorous; fruits scarcely 3 mm. long and wide .. .. 36. *E. brachyandra*

Leaves 10-20 cm. long, concolorous; fruits 6-10 mm. long and wide .. .. 39. *E. oligantha*

Leaves mostly lanceolate or broadly lanceolate and then more or less acute or acutely acuminate (3 or usually more times as long as wide, with usually at least 20 pairs of lateral veins):

Twigs decidedly pruinose; fruits constricted into a short neck below the expanded rim, with included valves .. .. 43. *E. cyanoclada*

Twigs not pruinose; fruits without a constricted neck:

Fruits mostly less than 5 mm. wide; if not, then wider than long or the walls very thin and not wrinkled:

Fruits cup-shaped with slightly included to shortly exserted valves .. .. 42. *E. tectifica*

Fruits hemispherical to more or less turbinate or broader than long, with usually strongly exserted valves .. .. 41. *E. microtheca*

Fruits 4.5-10 mm. wide, as long or longer than wide, with relatively thick and usually wrinkled sides:

Rim and disc of fruit together 2-3 mm. wide; leaves distinctly veined .. .. 37. *E. patellaris*

Rim and disc of fruit together 1-1.5 mm. wide; leaves with faint veins .. .. 40. *E. argillacea*

3. Bark more or less rusty or variegated rusty and light grey, at least on the upper part of the tree .. .. See trees with smooth bark, 2

2. Trees with a conspicuous amount of smooth, white, greyish, or pinkish, rarely brownish bark on the main branches and sometimes throughout, shed each year in flakes or strips; sometimes the amount of smooth bark inconspicuous, but then

the bark on the larger branches and on at least the upper part of the trunk more or less rusty and usually variegated with light grey or cream:

5. Bark on at least the lower part of trunk persistent, grey to dark grey, not readily broken away by the hand, and if so then grey beneath:

Persistent bark neatly cracked into small, nearly square pieces by vertical and horizontal fissures; leaves mostly relatively broad, often opposite, usually stiff and spreading, sometimes sessile or nearly so; fruits with included valves:

Leaves 2-5.5 cm. long; fruits 5-10 mm. long; rough bark sometimes only very close to base .. .. 8. *E. aspera*

Leaves larger, up to 15 cm. long, often deciduous; fruit 8-12 mm. long:

Entirely glabrous; leaves not cordate, sometimes narrow, never sessile, often very variable in breadth on the same tree .. .. 5. *E. clavigera*

More or less hispid or scabrous, particularly on the twigs and younger leaves; leaves more or less cordate, usually very similar in shape on the same tree, sessile or on some trees petiolate .. .. .. 6. *E. confertiflora*

Persistent bark (sometimes extending throughout or nearly throughout the tree) irregularly vertically fissured and becoming rugged towards the base, superficially more or less scaly; leaves relatively long and narrow, more or less drooping; fruits with more or less exserted valves:

Fruits not more than 4 mm. wide or else wider than long; leaves flexible, distinctly veined; smooth bark whitish or greyish .. .. 41. *E. microtheca*

Fruits 4.5-6 mm. wide, mostly longer than wide; leaves stiff, obscurely veined; smooth bark brownish .. .. 40. *E. argillacea*

5. Bark either smooth throughout or else the whole or part of the trunk or main branches with grey to yellowish or rusty bark, the outer layers readily torn away in long strips or rubbed away in thin flakes or scales, often rusty or yellowish beneath:

6. Fruits with exserted valves; bark smooth throughout:

Leaves sessile or nearly so, opposite .. .. 35. *E. apodophylla*

Leaves evidently petiolate, mostly alternate:

Fruits with a prominent erect disc; valves entirely exserted, their base level with the top of the disc:

Fruits subglobose with deltoid, incurved valves .. .. 31. *E. camaldulensis*

Fruits with an obconic calyx-tube and subulate, suberect, or slightly spreading valves .. .. 30. *E. herbertiana*

Fruits with a slightly convex to flat or descending disc or the disc quite obscure; valves inserted below the level of the rim:

Leaves always broadly ovate and more or less deltoid, glossy green, large (mostly 8-14 × 7-12 cm.) and on long petioles (3-5.5 cm.); buds 11-12 × 10 mm., subglobular; fruits 7-9 × 9-11 mm., the rim together with disc 1-1.5 mm. thick .. .. 34. *E. bigalerita*

Leaves broad or narrow, but usually smaller than above; if broad then dull green or yellowish green or more or less glaucous; petioles often short; buds smaller; fruits often smaller, the rim often narrower:

Inflorescence more or less terminal; fruits as broad as or broader than long, the calyx-tube often very short; leaves with 30-40 pairs of lateral veins, mostly narrow; low, scrubby trees or shrubs of the desert .. .. Some states of 41. *E. microtheca*

Inflorescence axillary; fruits as long as or longer than wide, rarely somewhat wider than long and then leaves broad; leaves with less than 30 pairs of lateral veins; small to large trees, in the latter case not desert plants:

Fruits 3-4 mm. long and almost as wide, coarsely lacunose .. .. 49. *E. umbrawarrensis*

Fruits longer or wider or both, smooth or finely wrinkled:

Leaves with very faint veins; scrubby or shrubby trees with broad glaucous intermediate leaves and small narrow adult leaves 4-8 × 1-2 cm. on petioles mostly 8-17 mm. long .. .. 32. *E. brevifolia*

Leaves distinctly veined, all broad on long petioles on small trees, sometimes narrow on shorter petioles on tall trees .. .. 33. *E. alba*

6. Fruits with included valves; bark at least partly persistent in most species:

Fruits ribbed; persistent bark somewhat compressible, composed of very many layers of very thin, small scales:

Persistent bark greyish; fruits 2 cm. or more wide .. .. .. 4. *E. miniata*

Persistent bark yellowish; fruits less than 1.5 cm. wide .. 3. *E. phoenicea*

Fruits not ribbed; persistent bark tessellated or scaly, the scales rusty beneath and mostly superficial:

Leaves ovate or oblong, rarely more than 3 times as long as wide:

Leaves opposite and more or less sessile, 2-6 cm. long .. .. 8. *E. aspera*

Leaves alternate or also opposite, distinctly petiolate, at least 8 cm. long:

Bark smooth and white or with some grey flakes near the base; leaves green, more or less shining .. .. 7. *E. grandifolia*

Bark partly scaly and variegated rusty and pale grey:

Fruits 9-15 mm. long .. .. 19. *E. latifolia*

Fruits 20-26 mm. long .. .. 20. *E. foelscheana*

Leaves lanceolate or narrowly lanceolate, the majority of them more than 3 times as long as wide:

Leaves very green and shining on the upper surface, paler and duller beneath; bark white for the greater part .. .. 17. *E. bleeseri*

Leaves dull green to yellowish green, not very different on the lower surface:

Fruits with rather thin, often polished and mottled walls, and thin, erect or spreading rim, mostly 8-15 × 8-12 or rarely up to 20 × 15 mm. but not much longer than wide; bark sometimes smooth and white nearly throughout .. .. 18. *E. dichromophloia*

Fruits with thick walls and thick, more or less erect rim, at least 15 mm. long or wide; smooth bark sometimes inconspicuous, rarely extending nearly to the base:

Fruits longer than wide .. .. 15. *E. terminalis*

Fruits as wide as or wider than long; smooth bark inconspicuous to absent (always?) .. .. 22. *E. cliftoniana*

KEY BASED ON SPECIMENS IN BUD AND FLOWER, WITH OR WITHOUT FRUITS

1. Calyx-tube equally 4-angled in flower and sometimes also in fruit, the angles more or less ribbed and produced at or below the top into lobes or teeth; flowers in axillary and also terminal 3-flowered umbels:

Buds 4-5 × 3-4 mm.; fruits 8-12 × 5-6 mm. with the angles and sometimes also the teeth rudimentary; lateral veins at an angle of 20°-30° with the midrib (a mallee) .. .. 1. *E. odontocarpa*

Buds 10-12 × 8-10 mm.; fruits 13-17 × 10-11 mm.; lateral veins at an angle of 45°-50° with the midrib (a tree) .. .. 2. *E. tetrodonta*

1. Calyx-tube neither toothed nor equally 4-angled; ribs absent or 1-3, or 6 or more, very rarely 4 and then unequally spaced; inflorescence various, more than 3-flowered except in *E. pachyphylla* and sometimes *E. aspera*:

2. Anthers versatile and also much longer than wide, more or less obovate-oblong or oblong, with parallel cells opening nearly throughout in longitudinal slits; filaments attached near the middle of the back of the anther, usually attenuated; bark variously tessellated or scaly, or partly or wholly smooth, long-fibrous in *E. jacobsiana*:

3. Operculum shorter to very much shorter than the calyx-tube; free part of calyx-tube nearly as long to as long as the adnate part, erect or spreading, with its rim distinctly above the level of the flat-topped ovary; fruits with included valves:

4. Free part of calyx-tube more or less saucer-shaped and very much wider than the ovary; operculum mostly very thin, sharply circumsciss: flowers axillary or along leafless branches, in short corymbose panicles or simple or compound umbels; fruit fragile, with thin, often venulose walls:

Pedicels shorter than the buds and fruits:

Leaves sessile, opposite, more or less cordate, scabrous .. .. 8. *E. aspera*

Leaves petiolate, usually alternate, never cordate, always glabrous and smooth .. .. 10. *E. papuana*

Pedicels much longer than the buds and fruits:

Leaves more or less hairy, at least on the midrib beneath, with 10-13 pairs of lateral veins, cordate, often sessile .. .. 6. *E. confertiflora*

Leaves glabrous, with 13-25 (rarely up to 30) pairs of lateral veins, prominently petiolate, not evidently cordate:

Leaves with 13-16 pairs of lateral veins; buds 12-13 × 7-9 mm.; fruit 10-18 × 8-14 mm. .. .. 7. *E. grandifolia*

Leaves with 18 or more pairs of lateral veins; buds 6.5-8 × 5-6 mm.; fruits 8-12 × 8-10 mm. .. .. 5. *E. clavigera*

4. Free part of calyx-tube more or less cup-shaped or tubular, about as wide as or not much wider than the ovary, so that the top of the receptacle is more or less U-shaped in section; operculum relatively thick and not sharply differentiated from the calyx-tube, from which it is rather irregularly circumsciss; fruits scarcely fragile, often woody; inflorescences terminal except in *E. phoenicea* and *E. miniata*:

5. Leaves with less than 20 pairs of lateral veins, sessile or nearly so and often amplexicaul, often with some kind of indumentum, usually not more than 3 times as long as wide:

Indumentum of bristly hairs persistent on the inflorescence and younger twigs; leaves mostly 5-10 cm. long with 9-12 pairs of lateral veins; fruit nearly as wide as long .. .. 12. *E. setosa*

Indumentum (if present) of chiefly rusty, powdery scales easily rubbed away, usually leaving some persistent, often silvery scales; bristles sometimes present on the twigs; leaves mostly at least 7 cm. long; fruit longer than wide:

Leaves with 6-10 pairs of lateral veins; at least twigs and lower surface of leaves rusty .. .. 13. *E. ferruginea*

Leaves with 12-15 pairs of lateral veins; indumentum absent or nearly so; twigs somewhat pruinose .. .. 14. *E. abbreviata*

5. Leaves with at least 20 pairs of lateral veins, prominently petiolate, rounded or cuneate at the base, glabrous in the adult state, often narrow:

Umbels solitary, axillary or on the old wood; pedicels 1-6 mm. long; fruit several-ribbed; leaves with up to 36 pairs of lateral veins, at least 2.5 times as long as wide:

- Calyx-tube of flower not pruinose, faintly ribbed, 5-7 mm. wide; pedicels slender, mostly 4-6 mm. long; fruits 1.1-1.2 cm. wide; leaves with 30-36 pairs of veins .. .. 3. *E. phoenicea*
- Calyx-tube of flower pruinose, strongly ribbed, 8-10 mm. wide; pedicels nearly as wide as to wider than long, often very short; fruits 2.5-5 cm. wide; leaves with 22-30 pairs of veins .. .. 4. *E. miniata*

Umbels terminal or subterminal, usually in corymbose panicles; fruits unribbed, or if so then on pedicels longer than 10 mm.; leaves of most species with 40 or more pairs of lateral veins:

- Calyx-tube strongly 8-ribbed in both flower and fruit .. 23. *E. ptychocarpa*
- Calyx-tube not ribbed, very rarely even striate:
  - Buds and fruits finely and closely wrinkled, nearly as wide as long, on slender pedicels 12-20 mm. long; buds 13-15 × 10-12 mm., narrowed to base; fruits 20-25 × 17-20 mm. .. .. 21. *E. porrecta*
  - Buds and fruits smooth or scurfy or papillose, on shorter pedicels, or else of different shape or size:
    - Leaves less than 3 times as long as wide:
      - Buds 5-6 × 4-5 mm.; fruits 9-15 × 8-14 mm. .. .. 19. *E. latifolia*
      - Buds 12-14 × 7-11 mm.; fruits 20-26 × 16-20 mm. .. 20. *E. foelscheana*
    - Leaves at least 3 times as long as wide:
      - Leaves mostly 6-9 × 0.8-1.4 cm., with very prominent reticulations between the lateral veins; buds 4-5 × 3 mm.; fruits 8-10 × 5-8 mm. .. .. 24. *E. jacobsiana*
      - Leaves larger; reticulations obscure:
        - Buds mostly not larger than 8 × 6 mm.; pedicels up to 5 mm. long; fruit with acute rim, not conspicuously woody, not scurfy, rarely more than 15 mm. long and usually less than 15 mm. wide:
          - Buds pyriform, 7-8 × 5 mm.; fruits about 1.5 times as long as wide, about 11-13 × 7-8 mm. .. .. 25. *E. nesophila*
          - Buds subglobose, 5-7 × 3-6 mm.; fruit not much longer than wide .. .. 18. *E. dichromophloia*
        - Buds at least 9 mm. long; pedicels sometimes long; fruit either 1.5-2.5 times as long as wide or else with blunt rim and more or less woody, commonly dull or scurfy, 1.5-4 cm. long, 10-25 mm. wide:
          - Leaves markedly paler beneath; buds about twice as long as wide:
            - Pedicels shorter or much shorter than the scurfy, whitish buds and fruits .. .. 16. *E. polycarpa*
            - Pedicels as long as or longer than the smooth, usually reddish buds and fruits .. .. 17. *E. bleeseri*
          - Leaves about the same colour on both sides; buds about 1.5 times as long as wide or shorter:
            - Pedicels mostly 5-17 mm. long; buds turbinate-obovoid, 9-14 × 6-9 mm.; fruit longer than wide .. .. 15. *E. terminalis*
            - Pedicels up to 6 mm. long; buds not seen; fruit as wide as or wider than long .. .. 22. *E. cliftoniana*

3. Operculum about as long as or longer than calyx-tube, the free part of which is very short; top of ovary more or less convex or domed (rarely nearly flat), from slightly below to much above the level of the rim; flowers in axillary umbels; fruits with flush or exserted valves; bark smooth:
   - Leaves sessile and opposite, more or less cordate; younger parts pruinose .. .. 35. *E. apodophylla*
   - Leaves petiolate, mostly opposite, more or less cuneate at the very base even if the leaf as a whole is somewhat cordate; younger parts usually not pruinose:
     - Operculum longer than the calyx-tube; top of ovary higher than the rim; fruit with prominent disc higher than the rim and more or less closely appressed to the entirely exserted valves:
       - Calyx-tube in both flower and fruit finely 1-3-ribbed, gradually narrowed to base; pedicels stout, up to 3 mm. long or rudimentary .. 30. *E. herbertiana*
       - Calyx-tube in both flower and fruit unribbed, abruptly rounded to slender pedicels, which are 3-8 mm. long .. .. 31. *E. camaldulensis*
     - Operculum about as long as calyx-tube; top of ovary not higher than the rim (sometimes higher after the stamens have fallen); fruit with an obscure or nearly flat or descending disc; base of valves below the rim:
       - Leaves mostly 4-8 × 1-2 cm., 3-6 times as long as wide, dull, with indistinct veins; petioles usually not more than 15 mm. long .. 32. *E. brevifolia*
       - Leaves longer or much wider or both, frequently much less than 3 times as long as wide; veins rather distinct; petioles 15-50 mm. long:
         - Buds 11-12 × 10 mm.; rim with disc 1-1.5 mm. wide in fruit 34. *E. bigalerita*
         - Buds narrower (up to 7 mm. wide) and usually shorter; rim of fruit (with disc) usually narrower .. .. 33. *E. alba*

2. Anthers basifixed (more or less versatile in *E. brachyandra* and sometimes slightly so in *E. pachyphylla*), reniform to ovoid or oblong, rarely much longer than wide, the cells (often not parallel) opening in pores or short slits, the openings commonly as wide or nearly as wide as long, sometimes nearly or quite confluent at the top and usually distinctly shorter than the cells; filaments attenuated upwards in some species, nearly equally thick throughout in others; bark usually grey to blackish, rough, persistent, neither tessellated nor rusty, sometimes smooth above, rarely throughout and then white:
   - Buds 18-25 × 13-20 mm.; fruits 13-17 × 18-30 mm., both with a short, several-ribbed calyx-tube; disc tall .. .. 50. *E. pachyphylla*
   - Buds and fruits much smaller, unribbed or with up to 4 faint ribs; their calyx-tube at least about half as long as themselves; disc flat or descending or obscure:
     - Leaves 1-3 times as long as wide, commonly obtuse or nearly so, if as much as 3 times then discolorous:
       - Leaves sessile and opposite; younger parts pruinose .. .. .. 46. *E. pruinosa*
       - Leaves all on long petioles, alternate or also opposite; younger parts not pruinose:
         - Buds about 2 mm. long and somewhat narrower; fruits about 2.5-3 mm. long and wide; leaves distinctly paler beneath, 5-8 × 2-4 cm. . 36. *E. brachyandra*
         - Buds about 7-10 × 5-6 mm.; fruits 6-10 × 6-9.5 mm.; leaves green or grey-green on both sides, mostly 10-20 × 5.5-12 cm. .. .. .. 39. *E. oligantha*
     - Leaves at least 3 times as long as wide, concolorous, often acute or acuminate:
       - Buds about 6 mm. wide, more than twice as long as wide; pedicels 6-11 mm. long; fruit at least 10 mm. long and 8 mm. wide .. .. 37. *E. patellaris*
       - Buds 2.5-5 mm. wide, 1-1.5 times as long as wide (up to 8 mm. long); pedicels up to 5 mm. long; fruit up to 9 mm. long and up to 6 mm. wide:

Lateral veins in 18-40 pairs at an angle of 40°-65° with the midrib, usually very faint in *E. argillacea;* buds 4-8 × 3-5 mm.; leaves mostly 8-15 cm. or more long on petioles 0.8-2.5 cm. long:

Operculum about half as long as calyx-tube; pedicels 2-5 mm. long; buds turbinate or obovoid to pyriform; fruits 4.5-9 × 4.5-6 mm.:

Lateral veins in 18-26 pairs, fairly distinct; operculum distinctly narrower than the widest part of the calyx-tube; fruit with included valves .. .. 43. *E. cyanoclada*

Lateral veins in 30 or more pairs, usually faint; operculum as wide as calyx-tube; fruits with flush to exsert valves .. .. .. 40. *E. argillacea*

Operculum distinctly more than half as long as calyx-tube and up to slightly longer than it; pedicels 0-3 mm.; buds ovoid or ellipsoid or more or less pyriform:

Anthers opening in rounded pores; buds more or less pyriform; lateral veins in 20-30 pairs; fruits cup-shaped with slightly included to slightly exserted valves, not wider than long .. .. 42. *E. tectifica*

Anthers opening in short slits; buds ellipsoid or ovoid; lateral veins in 30-40 pairs; fruits with usually prominently exserted valves, the calyx-tube more or less turbinate or saucer-shaped, commonly wider than long .. .. 41. *E. microtheca*

Lateral veins in 12-24 pairs at an angle of 25°-40° with the midrib, sometimes very faint; buds about 3-3.5 × 2.5-3.5 mm.; leaves mostly 5-10 cm. long; petioles 0.5-1.2 cm. long:

Leaves 3-5 times as long as wide with 12-17 pairs of veins; buds obovoid-globular, about 3.5 mm. long and wide, abruptly narrowed at base; pedicels 0-2 mm. long .. .. 45. *E. jensenii*

Leaves 5-14 times as long as wide, with 15-24 pairs of veins; buds turbinate-obovoid, 3-3.5 mm. long, about 2.5 mm. wide, more or less tapering to pedicels 1-3 mm. long:

Outer stamens without anthers; flowers in small, terminal and subterminal panicles; fruits with included valves .. .. 44. *E. normantonensis*

All (?) stamens with anthers; flowers in strictly axillary umbels; fruits with flush to exsert valves .. .. 49. *E. umbrawarrensis*

KEY BASED ON SPECIMENS IN FRUIT, BUT WITHOUT FLOWERS OR BUDS

1. Fruit with entirely included valves, their tips distinctly below the rim, sometimes nearly flush in *E. tetrodonta* which has a 4-toothed calyx-tube (*E. oligantha* and *E. tectifica* have variable valves and appear in both sections of the key):

2. Fruits with 4 or 8 angles or ribs (sometimes with subsidiary ribs added), which are sometimes produced at or below the rim into teeth or lobes:

Ribs or angles 4; fruit usually 4-toothed, less than 2 cm. long:

Fruits 8-12 mm. long; leaves 6-15 mm. wide with veins at an angle of 20°-30° with the midrib .. .. 1. *E. odontocarpa*

Fruits 13-17 mm. long; leaves 15-40 mm. wide, the lateral veins at an angle of 45°-50° with the midrib .. .. 2. *E. tetrodonta*

Ribs 8 or more; fruit at least 2 cm. long, commonly not toothed:

Fruits less than 1.5 cm. wide on slender pedicels up to about 5 mm. long in lateral umbels; cells 2, rarely 3; leaves with 30-36 pairs of lateral veins on petioles up to 1.5 cm. long .. .. 3. *E. phoenicea*

Fruits at least 2 cm. wide, with 3-5 cells; pedicels different from above; leaves with fewer or more numerous veins, on petioles 1.5-3 cm. long:

Leaves less than 15 cm. long with 22-30 pairs of veins; pedicels up to 5 mm. long and nearly as wide, or rudimentary; fruit usually 3-celled, in lateral umbels .. .. 4. *E. miniata*

Leaves more than 15 and up to 35 cm. long with 60-80 pairs of veins; pedicels 15-22 mm. long, slender; fruits 4- or 5-celled in terminal and subterminal inflorescences .. .. 23. *E. ptychocarpa*

2. Fruits not angled, ribbed, or toothed, sometimes faintly and irregularly striate or venulose:

3. Leaves sessile or subsessile and more or less cordate, mostly opposite, often more or less scabrous or hispid, not more than 3.5 times as long as wide, with not more than 20 pairs of lateral veins; petioles sometimes evident in *E. confertiflora* and *E. ferruginea,* but the cordate leaves have not more than 13 pairs of veins:

Fruits very thin-walled, less than 15 mm. long; inflorescences axillary or along leafless branches:

Leaves mostly 2-5 cm. long and 1-2 cm. wide, with 13-20 pairs of lateral veins; pedicels shorter than the fruits .. .. 8. *E. aspera*

Leaves mostly much larger (up to 15 cm. long and 10 cm. wide), with 10-13 pairs of veins; pedicels much longer than the fruits .. 6. *E. confertiflora*

Fruits more or less woody with thick walls, at least 15 mm. long; inflorescences terminal or nearly so:

Fruits about as wide as long; bristly hairs usually conspicuous on the twigs and sometimes on the leaves; leaves with 9-12 pairs of veins, mostly 5-10 cm. long .. .. 12. *E. setosa*

Fruits distinctly longer than wide; bristly hairs sparse or absent; leaves mostly 7-17 cm. long, often with fewer than 9 or more than 12 pairs of veins:

Leaves and twigs (except in extreme age) ferruginous with a close and dense indumentum of minute scales mixed with some short and often branched bristles; leaves with 6-10 pairs of veins; rim of fruit not spreading .. .. 13. *E. ferruginea*

Leaves and twigs glabrous or nearly so; leaves with 12-15 pairs of lateral veins; twigs somewhat pruinose; fruits with spreading rim . 14. *E. abbreviata*

3. Leaves petiolate, usually alternate, always glabrous, cuneate to broadly rounded (rarely somewhat cordate, but then with at least 13 pairs of lateral veins):

4. Fruit 8 mm. or more long, usually widest at or below the middle; valves always deeply enclosed:

Fruits rather fragile with thin walls throughout and sometimes venulose, up to 18 mm. long, in axillary inflorescences or crowded along leafless branches; leaves with not more than 40 pairs of lateral veins:

Pedicels as long as or longer than the fruits; lateral veins up to 30, but rarely more than 25 pairs; leaves mostly 1.5-4 (up to 6) times as long as wide:

Lateral veins in 18-30 pairs; fruits 8-12 × 8-10 mm. .. .. 5. *E. clavigera*

Lateral veins in 13-16 pairs; fruits 10-18 × 8-14 mm. .. 7. *E. grandifolia*

Pedicels shorter than the fruit; lateral veins in 28-40 pairs; leaves usually 5 or 6 (up to 8) times as long as wide .. .. 10. *E. papuana*

Fruits with thick to very thick, more or less woody walls, sometimes thin and acute at the rim, 8-40 mm. long, in more or less terminal inflorescences; lateral veins in 40 or more pairs except in *E. porrecta, E. latifolia,* and *E. foelscheana,* which have as few as 30 pairs:

Fruits finely and closely wrinkled, broadly ovoid to subglobose, 20-25 × 17-20 mm., on slender pedicels 12-20 mm. long; leaves mostly 2-3.5 times as long as wide .. .. 21. *E. porrecta*

Fruits not as above, not wrinkled except when very young, and if subglobose then with much shorter pedicels; leaves mostly narrower or wider:

Leaves mostly 1.5-2, rarely up to 3 times as long as wide:

Fruits 9-15 × 8-14 mm., nearly as wide as long .. .. 19. *E. latifolia*

Fruits 20-26 × 16-20 mm., distinctly longer than wide .. 20. *E. foelscheana*

Leaves at least 3 times as long as wide; lateral veins in 40 or more pairs:

Reticulations prominent between the lateral veins, especially on the whitish lower surface; leaves mostly 6-9 × 0.8-1.4 cm.; fruits 8-10 × 5-8 mm. .. .. 24. *E. jacobsiana*

Reticulations obscure or invisible; leaves mostly longer and wider; fruits longer or wider, or both:

Fruits about 1.5-2.5 times as long as wide:

Leaves about the same colour on both sides, often somewhat yellowish; venation indistinct; fruit 17-40 × 13-23 mm. with a thick, usually obtuse rim .. .. 15. *E. terminalis*

Leaves much paler and duller on the lower surface with distinct veins; fruits 7-15 mm. wide, with usually a thin rim:

Fruits about 11-13 × 7-8 mm. .. .. 25. *E. nesophila*

Fruits 15-30 × 10-15 mm.:

Pedicels up to 12, but commonly less than 10 mm. long; fruit scurfy .. .. 16. *E. polycarpa*

Pedicels 13-20 mm. long; fruit not scurfy, often polished 17. *E. bleeseri*

Fruits from rather shorter than wide, up to nearly 1.5 times as long as wide:

Fruits mostly rather longer than wide, with a thin, erect, or spreading rim and a short neck, mostly 8-15 but up to 20 mm. long, mostly 8-12 but up to 15 mm. wide, mostly smooth and polished and more or less mottled .. .. 18. *E. dichromophloia*

Fruits shorter than to as long as wide with an indistinct neck and a thick, flat or depressed rim, 15-20 mm. long, 20-25 mm. wide, not polished (always?) .. .. 22. *E. cliftoniana*

4. Fruit up to 7 mm. long, or if longer and up to 10 mm. long then widest at or just below the top with the valves inserted shortly beneath the rim and their valves often flush or partly exserted:

Leaves not more than 3 times as long as wide, more or less decidedly obtuse; lateral veins in 12-20 pairs:

Fruits 2.5-3 mm. long and wide; leaves up to 8 cm. long .. 36. *E. brachyandra*

Fruits 6-10 mm. long and wide; leaves 10 cm. or more long . 39. *E. oligantha*

Leaves at least 3 times as long as wide and if only 3 times then acute or acuminate; lateral veins up to 30 pairs:

Lateral veins at an angle of 25°-40° with midrib, in 15-20 pairs; fruits 3-4 mm. long and wide .. .. 44. *E. normantonensis*

Lateral veins at an angle of 45°-60° with midrib, in 18-30 pairs; fruits 4-7 mm. long:

Fruits constricted below the excurving rim .. .. .. 43. *E. cyanoclada*

Fruits not constricted below the erect or incurving rim .. 42. *E. tectifica*

1. Fruits with the tips of the valves flush with the rim to prominently exserted, never 4-toothed:

Leaves sessile or nearly so, opposite or nearly so, commonly cordate and pruinose:

Fruits 3-4 × 4-5 mm., in axillary umbels .. .. 35. *E. apodophylla*

Fruits 7-10 × 5-8 mm., in more or less terminal small panicles .. 46. *E. pruinosa*

Leaves prominently petiolate, alternate or sometimes also opposite, mostly more or less cuneate or rounded at the base:

Fruit 13-17 × 18-30 mm. with a short, several-ribbed calyx-tube and a tall and thick disc .. .. 50. *E. pachyphylla*

Fruits up to 13 mm. long and 11 mm. wide; calyx-tube with at most 3 ribs, sometimes nearly as long as the fruit:

Disc distinctly higher than the rim, erect or insloping, reaching to the base of the entirely exserted valves:

Valves erect or nearly so or slightly spreading; calyx-tube obconic with 1-3 fine ribs, about as wide as long; pedicels 0-3 mm. long .. 30. *E. herbertiana*

Valves more or less following the curvature of the sub-globular fruit, incurved from a slightly excurving broad base; calyx-tube unribbed, usually broader than long, rounded at base; pedicels at least 3 mm. long . 31. *E. camaldulensis*

Disc very shortly convex to descending or obscure; valves inserted at or below the level of the rim; calyx-tube occupying much the greater part of the length of the fruit except in *E. microtheca*:

5. Leaves usually broad, with 10-18 pairs of lateral veins, on petioles 25-70 mm. long; if petioles as short as 15 mm. and leaves narrow, then the latter with no more than 15 pairs of veins:

Intramarginal vein of leaf distinctly less than 1 mm. from the margin with which it is more or less confluent for usually a considerable distance above the base; leaves always alternate from as long to twice as long as wide with 12-18 pairs of lateral veins; umbels terminal or subterminal, more or less paniculate; fruits 6-10 × 6-10 mm. .. .. 39. *E. oligantha*

Intramarginal vein of leaf mostly more than 1 mm. from the margin and distinct from it almost or quite to the base, sometimes double; leaves often approximated in pairs or even opposite, broad or narrow, with 10-12 pairs of lateral veins when broad and up to 15 pairs when narrow; umbels axillary, solitary, or on the older parts of the twigs:

Leaves 1-1.5 times as long as wide, more or less glossy, rather obscurely veined, commonly with a double intramarginal vein; fruits 7-9 × 9-11 mm., wider than long, on short, very stout pedicels or sessile; rim and disc together between 1 and 1-5 mm. wide .. .. 34. *E. bigalerita*

Leaves 1.3-7 times as long as wide, usually dull or subglaucous, prominently veined, rarely (if ever) with a double intramarginal vein; fruits commonly smaller and frequently no wider than long, often with a thinner rim and sometimes with slender pedicels; rarely the fruit up to 8 × 10 mm. and then very similar to the preceeding species .. .. 33. *E. alba*

5. Leaves at least 3 times as long as wide, on petioles less than 25 mm. long, or if as long as 25 mm., then with at least 20 pairs of lateral veins:

Veins rather distinct in 20-30 pairs at an angle of 45°-55° with the midrib; petioles 10-25 mm. long; fruits 4-6 × 4-5 mm., cupshaped with thin walls, as long as or longer than wide, sometimes with included valves .. 42. *E. tectifica*

Veins more numerous or fewer or at a more acute angle, sometimes very faint; petioles 5-20 mm. long; fruits sometimes with relatively thick walls or the calyx-tube wider than long:

Leaves with 12-25 pairs of lateral veins, sometimes quite faint, usually at an angle of 30°-40° (up to 50°) with the midrib, mostly 4-10 cm. long, 3-10 times as long as wide; petioles 5-12 mm. long; pedicels 0-2.5 mm. long; fruits 3-7 × 3-6 mm., about as wide as long:

Fruits 3-4 mm. long, lacunose on the walls, rather gradually narrowed to the pedicel which is 2-2.5 mm. long; leaves with 15-24 pairs of very faint veins, 5-10 times as long as wide .. .. 49. *E. umbrawarrensis*

Fruits sometimes larger, smooth or finely and closely wrinkled, more or less abruptly rounded at the base; pedicels 0.2 mm. long; leaves with up to about 20 pairs of veins, 3-6 times as long as wide:

Fruits 5-7 × 5-6 mm., rim about 0.5 mm. wide or rather more; petioles 8-17 mm. long; leaves commonly acute .. .. 32. *E. brevifolia*

Fruits 3.5-5 × 3.5-5 mm., rim much less than 0.5 mm. thick; petioles 5-11 mm. long; leaves commonly obtuse .. .. 45. *E. jensenii*

Leaves with 30 or more pairs of veins at an angle of 40°-65° with the midrib, mostly 8-20 cm. long, usually more than 4 times as long as wide; pedicels and fruits variable:

Calyx-tube as long as or longer than wide, rather prominently wrinkled; rim about 0.5 mm. thick; fruit 4.5-9 × 4.5-6 mm., not wider than long .. .. 40. *E. argillacea*

Calyx-tube commonly as wide as or wider than long, not wrinkled; rim very thin, sometimes spreading horizontally and then apparently wider; fruits 3-4.5 × 3-5.5 mm., at least the calyx-tube usually wider than long .. .. 41. *E. microtheca*

APPENDIX I

As stated in the Introduction, the primary object of the investigation that led to this paper was the establishment of the correct names of the species of *Eucalyptus* found in the northern part of the Northern Territory. This led to a preliminary revision of several groups in the genus, the more important results of which — so far as they are concerned with taxonomy, nomenclature, and general distribution — have been discussed in the earlier part of this paper. However, a number of other points arose during the investigation that seem worthy of discussion. They are mostly of a rather theoretical nature, though they have a direct bearing on taxonomic method, on plant geography, and on phylogeny. References in the following pages are to the Bibliography at the end of the Appendix.

Graphical methods have been used to illustrate the distinctiveness of certain groups of species. These diagrams were prepared purely as an experiment after the orthodox taxonomic work had been completed and are intended merely as illustrations. However, Mr. P. B. McGovern, Biometrician, Department of Agriculture and Stock, Brisbane, kindly examined the data from which Figure 2 was prepared, and he reported that the difference between the length:breadth ratios of the leaves of *E. dichromophloia* and *E. latifolia* is statistically highly significant. From inspection of a series of measurements, the ratio 3:1 appeared to separate the two species fairly sharply, but Mr. McGovern reports that a more precise discrimination is given by the formula

$$x = l - 5.44B,$$

where l and B are length and breadth respectively. The value x is algebraically greater than —102.25 for *E. dichromophloia,* algebraically less for *E. latifolia.* That is (introducing a slight approximation), if the expression $2l - 11B + 204$ is greater than zero, the leaf is from *E. dichromophloia;* if less, it is from *E. latifolia.* In Figure 2, the unbroken line represents the expression without the approximation. If classification were to be attempted on the basis of measurements of a single leaf, the proportion of misclassifications in either species would be about 5 per cent. on the average. The greater the number of leaves available, the less the chance of misidentification; if the average of four leaves were taken, the error would be less than 1 per cent. However, it should be mentioned that border-line examples were carefully looked for when the diagram was prepared and all those found were plotted; they may suggest a higher proportion of such leaves than is really the case. Figure 3 shows that leaves of intermediate shape between those characteristic for each species can be distinguished by the position of the intramarginal vein; the leaf of *E. dichromophloia* plotted at the extreme left is probably a late intermediate leaf which has not been plotted on the previous figure.

Figure 1 has been prepared from 35 leaves representing 10 collections of each of the seven species plotted, except for *E. gilbertensis* of which only three collections are available; five collections of each are represented by five leaves each, the other five by two each. While such a limited number of readings is scarcely amenable to statistical treatment, I believe that the resultant diagram gives a fairly accurate impression of the correlation between the species of the characters used. Random sampling of all available material is impossible because of the high proportion of damaged or deformed leaves. A study of a wide range of specimens usually leads to an opinion as to what is the "typical" form of an organ and the "normal" amount of variation which may be expected. "Exceptional" cases are those rarely met with which exceed the bounds of "normal" variation. Often they are starved, gigantic, deformed, or otherwise physiologically abnormal organs; they may be found in any or every species, and though they may be important when the identification of meagre specimens is attempted, little importance should be attached to them when studying specific limits.

Figure 1 illustrates a trend that has been observed in several groups of closely allied forms, which is that increase in the length/breadth ratio is associated with an increase in the number of lateral veins. The correlation is not found with unrelated species; for example, *E. foelscheana* has leaves up to twice as long as broad but with at least 30 pairs of veins, a number not found in the *Clavigerae* unless the leaves are at least 4.5 times as long as broad. Juvenile leaves of all species of the *Clavigerae* are relatively broad and have few veins; those of the different species resemble one another closely except for differences in indumentum and size. That the species distinguished here are not ontogenetic stages of a single species is shown by the correlation of other characters (indumentum, length of pedicel, size of buds and fruits, nature of bark) with the different leaf forms; some of the correlations are shown on the diagram.

Since seedlings have broad, opposite, horizontal leaves with few veins, very short petioles, and a certain amount of indumentum, it may be presumed that these characters are relatively primitive and that other characters are derived ones. On this assumption, the most primitive living member of the group is *E. confertiflora,* from which there has been a progressive evolution towards the prominently petiolate, alternate, vertical, many-nerved, glabrous leaves of *E. tessellaris.* The structure of the seed (not known in *E. gilbertensis*) suggests a progressive thinning of the margin from *E. confertiflora, E. aspera, E. grandifolia,* and *E. clavigera* through *E. papuana* to the distinctly scarious margins found in *E. tessellaris.* Other differences between the species are not so closely correlated with this trend, but long pedicels and sessile or subsessile leaves are found only in broad-leaved species.

The distribution maps summarize the known geographical distribution of 51 species, all but one of which (*E. gummifera,* map 5*C*) are found in the northern part of the continent; all species known from the northern part of the Northern Territory are mapped, but many species from the northern parts of Western Australia and Queensland are not mapped. The maps have been based on the actual examination of herbarium specimens; those in the Queensland Herbarium provided most of the localities for some species. Where there appeared to be no risk of misidentification, a few gaps have been filled in from the citation of localities by Blakely (1934) (shown by open circles) and from my own observations in the field (Blake unpublished data 1935-1947) (shown by half-open circles). A few localities have been mapped from Maiden's published figures which have been treated as specimens examined. [After the paper was completed more field work and the acquisition of many more specimens have added to the knowledge of the distribution of some species.]

Some species are known only from a very few collections or from collections from a very few localities; these have been discussed previously and include *E. abbreviata* (map 7*D*), *E. bleeseri* (map 12), *E. cyanoclada* (map 30*C*), *E. gilbertensis* (map 4*C*), *E. herbertiana* (map 23*A*), *E. jacobsiana* (map 7*C*), *E. nesophila* (map 7*A*), and *E. porrecta* (map 7*B*). Relative accessibility of both general locality and particular habitat, conspicuousness of species, availability of material for specimens, and vagaries of collectors are among the factors that determine the representation of species in the herbarium; some of the commonest or most distinctive species are poorly represented because they soon become well recognized in the field. The importance of accessibility is shown by the readiness with which the position of the road between Darwin and Alice Springs can be seen on maps 3, 11, 13, and 17, and the part of this road between Darwin and Mataranka on maps 1, 2, and 4*A*. Very few specimens have been seen from Western Australia south of the Kimberley Division; there are no records from the extreme south-east part of the Northern Territory nor from the interior of what is now called Arnhem Land.*

A study of the distribution of the species of *Eucalyptus,* imperfectly known as it is in many respects, leads to the following conclusions:

1. Several species are so widely spread over a large area of northern Australia as to suggest that this is a definite vegetation region. This suggestion is strengthened by (or perhaps arose from) experience in the field and detailed study of other groups. The distribution maps of certain genera of grasses of the predominantly tropical subtribe *Andropogoninae* published previously (Blake 1944) have a similar general pattern and so have the distribution of such families as Combretaceae and such genera as *Brachychiton* (Sterculiaceae), *Ficus* (Moraceae), and *Fimbristylis* (Cyperaceae).

2. Some species occupy extremely restricted areas, though each may be fairly common in that area (*E. apodophylla,* map 22*A*).

3. A few widely distributed species are rare; the localities in which they occur are widely scattered and each occurrence is very restricted in area; *E. jensenii* (map 27) is a striking example, and *E. aspera* (map 4*B*) and *E. normantonensis* (map 30*D*) may not be very different.

4. Geographical distribution and taxonomic relationship do not bear a consistent relationship. Closely allied species sometimes occupy contiguous or slightly overlapping areas, such as *E. pruinosa* and *E. melanophloia* (map 29) and *E. oligantha, E. patellaris, E. argillacea,* and *E. leptophleba* (maps 25, 28, and 30). Sometimes one or more such species occupy an area almost or quite included in that of its nearest ally (*E. shirleyi* and *E. melanophloia,* map 29), or the areas occupied may be widely distinct (*E. apodophylla* and *E. houseana,* map 22). Quite commonly, the area of a species is for the most part common to that of its nearest ally or several closely allied species may share a large part of the total area occupied by the group; this is well shown by the species of the *Clavigerae* (maps 1-4).

5. The species found beyond Australia belong to diverse groups (map 15).

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* The name Arnhem Land (Arnhem's Land, Arnheim Land, Arnheim's Land) has been used to indicate a greater or smaller part of the northern part of the Northern Territory. The name was originally bestowed on the land adjacent to the extreme northern coastline along which the ship *Arnhem* sailed in 1623. Mueller commonly used it for any or every part of the Northern Territory north of about 18° S. lat. except, perhaps, the part south of the Gulf of Carpentaria. On most maps published during this century the name refers to the broad peninsula north of the mouths of the Victoria and Roper Rivers, which is north of about 15° S. lat., and it is in this sense that the name was used by Jacobs (1934). Nowadays, the official use of the name is restricted to the Reserve for Aborigines, which occupies nearly the eastern half of this peninsula.

6. Widely spread species tend to show "preferences" for certain habitats though the "preferences" may alter towards the limits of their range; discontinuity of distribution is correlated with discontinuity of habitat.

7. Any explanation of the present distribution must take into account the history and development of the genus as a whole.

8. A classification involving the recognition of geographical races must take into consideration all these features of distribution.

Factors Influencing the Distribution of the Species

It is generally believed that the primitive angiosperms were evolved in early or middle Cretaceous time. The Myrtaceae are by no means primitive and it may be assumed that they arose much later, though they are presumed to have become more or less cosmopolitan by the end of the Cretaceous. At this time and in early Tertiary time, the surface of Australia seems to have been an almost perfect peneplain (David 1932), so that no serious physiographic or climatic barriers were placed in the way of a regular and wide distribution of existing species of plants. Since the end of the Miocene there have been cyclic changes in climate (Whitehouse 1940; Browne 1945) and some considerable earth movements (David 1932). In the Pliocene, two arid phases occurred and the Kosciusko Uplift produced great changes in altitude, particularly towards the south-east and east. Throughout the Pleistocene the climate appears to have been consistently much more humid than at present and there were two periods of low temperatures ("ice ages") with some small glaciated areas in the south. Towards the end of the Pleistocene, temperatures rose and rises in sea-level finally separated Tasmania and New Guinea from the Australian mainland. The increase in temperature continued into early Recent time and became associated with a widespread drop in rainfall. This increase in aridity produced desert conditions over a very large part of the continent. The desert was formerly much more extensive than at present (Blake 1938; Whitehouse 1940; Browne 1945; Crocker and Wood 1947) and Crocker and Wood have estimated that the period of maximum aridity occurred between 4000 and 6000 years ago. This was followed by a very marked increase in rainfall, which has since decreased to some extent.

Except for Whitehouse's account of the eastern part of the Barkly Tableland in the paper cited above, there are no published data on the past climate of the northern part of the Northern Territory. It would appear that there has been relatively little earth movement since the Cretaceous. Laterization (Pliocene?) was very widely spread. To judge from the similarity between the river terraces of the Katherine-Daly river system and the middle parts of the Adelaide and Roper Rivers with the terraces of Queensland rivers, this part of the continent must have shared in the heavy rains of the Pleistocene; further evidence is afforded by the huge areas of alluvium occupying portions of the Barkly Tableland, now an area of inland drainage. The numerous, small, isolated patches of monsoon forest ("jungle") scattered through the area may indicate a recent drop in rainfall. Their position, constitution, and distribution suggest that they are relicts, not developing communities such as some of those described from eastern Queensland (Blake 1938, 1941). This would suggest that in the relatively recent past the country was capable of supporting a much more mesic vegetation than at present. The remnants are often found on stony slopes or scarps, such a substrate apparently providing better water conditions (Blake 1941) and also probably acting as a partial protection from fires; other communities are associated with springs or occur on river banks. However, the composition of these "jungles" and that of the monsoon forests of northern and eastern Queensland is very similar; few species and very few genera found in the Northern Territory have not yet been found in Queensland* and many of the genera are also found in New Guinea. This wide distribution suggests that the communities are relicts from at least the Pleistocene and they may indicate the position of the refuges for some of the more mesic vegetation during the arid phase.

The Myrtaceae

Three great groups (tribes) of the Myrtaceae are now recognizable, the Myrteae with fleshy fruits, the Leptospermeae with dry, capsular fruits, and the Chamaelaucieae with dry, indehiscent, and unilocular one- or two-seeded fruits. (A fourth group, the Lecythideae, has been included with the Myrtaceae by some botanists, but this is now generally treated as a separate family, the Lecythidaceae, or as two separate families, Lecythidaceae and Barringtoniaceae.) It has generally been believed that the Myrteae represent the ancestral type. As mentioned previously, the family is supposed to have been more or less cosmopolitan at the end of the Cretaceous. At the present day, the Myrteae are nearly restricted to the tropics and subtropics; a very large number of species has been referred to the genera *Eugenia* and *Myrtus*, a considerable number of which is found in the area including south-eastern Asia, Malaysia, Australia, New Caledonia, and New Zealand. (Much difference of opinion still exists about the generic limits in the Myrteae; the names *Eugenia* and *Myrtus* are used here in the same sense as they have usually been used in Australian literature (Bentham 1867, 1869), though it is recognized that, on the whole, the American species and *Myrtus communis* (to which the names were first applied) differ from those of the Asiatic-Australian region.) The Leptospermeae are also widely spread, though almost confined to the Australian-Malaysian region, but the Chamaelaucieae are confined to Australia, chiefly to the south-western part of the continent.

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* Two noteworthy exceptions are the discovery during the N.A.R.S. Expedition of 1946 of the first species of *Horsfieldia* (Myristicaceae) and *Vavea* (Meliaceae) known from Australia; these will be discussed elsewhere.

The Leptospermeae have differentiated into five more or less distinct groups (subtribes)—Leptosperminae, Baeckeinae, Metrosiderinae, Eucalyptinae, and Beaufortiinae. They are most abundant in Australia, to which the last subtribe is confined, but some genera of the first three are widely distributed.*

This rich differentiation of the tribes and the wide distribution of some of the genera suggest that it must have differentiated fairly early in the history of the family, and that such genera as *Leptospermum* and *Metrosideros* must have arisen while Australia, New Guinea, New Caledonia, and New Zealand were in contact, that is, probably not later than the end of the Cretaceous. The Eucalyptinae, being absent from New Zealand and New Caledonia, may be presumed to have arisen at a later date, though Herbert (1935) has suggested that the absence of *Eucalyptus* from New Zealand is due to climate.

The paucity and unreliability of the fossil record makes any attempt to reconstruct the early history of the Eucalyptinae highly conjectural. Numerous leaf impressions from Cretaceous and Tertiary rocks in Europe, North America, and Australia and some fruits from the Northern Hemisphere have been referred to *Eucalyptus*, but it is most unlikely that those from the Northern Hemisphere really belong here (Maiden 1922; Berry and others quoted by Maiden 1922), and to judge from published figures, it is highly questionable whether some of those from Australia are correctly placed; others are very strongly suggestive of the genus. All these appear to be of Tertiary age, although a Cretaceous age was assigned to several when first described. It would seem that the genus had acquired considerable diversity in southern Australia and Tasmania in Pliocene time, and leaves resembling those of many of the *Corymbosae* are amongst those found in Tasmania where the group is no longer found. However, leaves of some of the living members of this group and some allied groups so closely resemble those of some living species of *Angophora*, *Eugenia*, and other diverse genera as to render very hazardous the determinations of single leaves. *Eucalyptus* has also been recorded from the Pliocene of northern Netherlands New Guinea (David 1932).

It is not proposed to discuss in detail the theories of origin and development of *Eucalyptus* put forward by Deane (1896), Cambage (1913), or Andrews (1913). The *Corymbosae* have usually been considered to be the most primitive type because of a fairly close correspondence in appearance and venation of the leaf to Australian species of *Eugenia;* to this may be added the more or less fleshy nature of the immature fruits in some species. However, the prevalence of winged seeds and the frequent occurrence of peltate leaves on young plants (sometimes present on adult trees in a very few species) do not appear to be primitive characters; the structure of the inflorescence (a panicle of umbels) differs from that of *Eugenia* (a simple or dichotomous or trichotomous cyme); the number of ovary cells (four or five, less commonly three) is higher than in *Eugenia*, which usually has a two-celled ovary; the setose indumentum, so characteristic of at least the juvenile stages of the *Corymbosae* and its parallel development in *Angophora*, is at least rare in *Eugenia*; and finally, there is nothing in *Eucalyptus* or *Angophora* to compare with the great, fleshy, sometimes more or less united cotyledons of *Eugenia*.

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* Examples are (1) Leptosperminae: *Leptospermum* (Australia, New Zealand, Malaysia); *Melaleuca* (Australia, New Caledonia, New Guinea, some other parts of Malaysia, and Indo-China). (2) Baeckeinae: *Baeckea* (Australia, New Caledonia, through Malaysia to southern China). (3) Metrosiderinae: *Metrosideros* (Australia, New Zealand, New Caledonia, New Guinea); *Tristania* (Australia, New Caledonia, New Guinea, through other parts of Malaysia to Burma).

These differences are more striking than the resemblances, and suggest that the Eucalyptinae could not have arisen directly from the Myrteae. It is true, however, that the Metrosiderinae and Eucalyptinae are more like some genera of the Myrteae (including *Eugenia*) than are the other subtribes of the Leptospermeae because of the prevailing combination of large leaves, pedunculate flowers, numerous stamens, and seeds with the radicle shorter than the cotyledons; also versatile anthers with parallel cells dehiscing in longitudinal slits and opposite leaves are found in all the genera. The Eucalyptinae (*Angophora* and *Eucalyptus**) differ from the Metrosiderinae (about 12-15 genera) by having the petals attached by a broad base (either distinct from one another or fused together), not contracted at the base. There is a close resemblance in foliage, stamens, ovary, and fruit between *Metrosideros*, *Angophora*, and *Eucalyptus* and in foliage and flowers between species of these genera and some species of *Eugenia*. Also, it is worthy of mention that some species of *Eugenia* have a coriaceous rather than a fleshy fruit, not so very different in texture from immature fruits of *E. terminalis* and other coarse-fruited species, and that *Backhousia* (Metrosiderinae) has indehiscent fruits. Some of the characters frequently stressed as characteristic of *Eucalyptus* are found in widely diverse genera. For example, some species of *Angophora* (Eucalyptinae), *Tristania*, *Syncarpia* (Metrosiderinae), *Myrtus*, *Eugenia*, and *Psidium* (Myrteae) have smooth, deciduous barks, and at least one species of *Tristania* (*T. conferta*) has rough, persistent bark on the lower part of the trunk and smooth, deciduous bark above; an operculum-like calyptra of fused sepals falling off in its entirety is characteristic of *Acicalyptus* (Metrosiderinae), *Calyptranthes*, and *Eugenia* sect. *Cleistocalyx* (Myrteae); united petals falling off as a calyptra (operculum) are characteristic of *Eugenia* sect. *Syzygium*; and divaricate anther cells characterize *Eugenia* sect. *Acmena*.†

In *Eucalyptus* itself, the great majority of species has no trace of sepals. However, in *E. tetragona* and some other species placed by

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* A peculiar third genus, *Eucalyptopsis* C. T. White has recently been recognized in New Guinea.

† *Cleistocalyx* Bl., *Syzygium* Gaertn., and *Acmena* DC. have been treated as distinct genera by some botanists.

Blakely (1934, pp. 13-14) in series *Eudesmiae,* the sepals are quite distinct and take the form of four persistent lobes or teeth, which are very prominent and quite broad on the young bud but tend to be much less distinct on the fruit; the operculum is formed entirely of the petals (cf. Brown 1814, pp. 599-600), the fused margins of which appear to be indicated by the four ridges apparent on at least the young bud. The mature operculum is almost petaloid in the peculiar *E. curtisii* (a local endemic in south-eastern Queensland), but is much coarser in the other species examined. In many species of other groups two opercula have been observed, a fragile outer one cast off before anthesis and usually when the bud is quite young, and a firmer inner one that becomes sharply circumsciss from the calyx-tube at anthesis. It is not known what proportion of the species has the outer operculum, but it is certainly much higher than was formerly supposed, and it is undoubtedly formed of the fused sepals; as first described by Maiden (1917, 1923), the outer operculum of *E. brachyandra* splits into four or five pieces before being shed.* In *E. citriodora* and *E. maculata* both the opercula are of firm texture and the outer is shed only shortly before the inner. In other species of the *Corymbosae,* the outer operculum tends to be thicker than the inner and to be only tardily or irregularly circumsciss; the inner operculum is thinner or much thinner in texture, sometimes quite distinct, but usually more or less strongly fused to the outer one. The point of the (outer) operculum is at least sometimes distinctly though minutely four-lobed in *E. setosa.*

The primitive unit of inflorescence appears to be a three-flowered cyme pedunculate in the axils of the leaves of an ordinary vegetative twig. The cyme may be reduced to one or two flowers, but in most species it has been altered to an umbel of few or many flowers. In many species, paniculate inflorescences have resulted from the shortening of the internodes of the twigs accompanied by reduction and finally the loss of the leaves at least in the upper part. The primitive three-flowered cyme persists (or sometimes occurs as a result of secondary reduction?) as a regular feature of many quite dissimilar species, such as *E. odontocarpa, E. tetrodonta, E. viminalis, E. rubida,* and *E. pachyphylla,* and is occasionally met with in many others; reduced cymes are usual in such unrelated species as *E. globulus* and *E. macrocarpa* and are occasionally found in some of those previously mentioned and in some paniculate species.

The leaves of *Eucalyptus* are very varied in shape, venation, and arrangement. However, the juvenile leaves seem to be constantly opposite, dorsiventral, sessile or shortly petiolate, and with few lateral veins, and these presumably represent the ancestral type. But the juvenile leaves vary also; the peltate leaves characteristic of some *Corymbosae* appear to be derived from decurrent leaves through the cordate condition; an indumentum of bristly or stellate hairs is also characteristic of some *Corymbosae* and some of the species placed by Blakely in the *Eudesmiae*.*

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* Maiden mentioned five pieces, but on some buds the outer operculum is shed as **four pieces.**

Some trends in the evolution of the leaves have been described in the early part of this appendix, but it is not known how universal these trends are. Neither embryological nor cytological studies have thrown much light on the evolution of the genus (Mauritzon 1939; Smith-White 1948).

If the ancestral type combined all characters that appear to be primitive, then we would expect a plant with opposite, few-veined, dorsiventral leaves, axillary three-flowered inflorescences, four calyx-lobes, some indication of four petals, versatile anthers with parallel cells opening in longitudinal slits, and a four-celled ovary; since the fruit was derived from a fleshy type, unwinged seeds might be expected. Of living species, *E. tetrodonta* agrees as to inflorescence, calyx, petals, anthers, ovary, and seeds, but the leaves are isobilateral and only irregularly opposite. But the primitive inflorescence is rarely seen in the Australian Myrteae or in the Metrosiderinae, in both of which the characteristic inflorescence is a more or less terminal dichotomous or trichotomous cyme. It seems that a compound terminal inflorescence was developed early in the history of the family and became particularly prevalent in the Australian-Malaysian region, with the primitive type persisting beside it or becoming reduced to give the solitary and more or less sessile axillary flowers characteristic of the Chamaelaucieae and some subtribes of the Leptospermeae. The terminal inflorescence sometimes becomes axillary in fruit by the continued growth of the shoot in the axil of one of the leaves immediately below the inflorescence.

If the interpretation of the Australian fossils mentioned above is correct, then some differentiation in the genus must have occurred while Australia had a relatively homogeneous topography and climate. Since six species, belonging to four distinct series, are found in both Australia and New Guinea (map 15), these species and likewise the groups to which they belong must have been differentiated before the separation of New Guinea, in late Pleistocene time. The fact that no endemic species occurs in southern New Guinea suggests that the genus did not occur in New Guinea previous to the appearance of the six species mentioned above and that no speciation has occurred since.* This would suggest that the species actually entered New Guinea in Pleistocene time. The entry of *E. alba* into Timor may have taken place by way of New Guinea along the route suggested by Lam (1938).

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* The *Eudesmiae*, as limited by Blakely, appear to be a rather heterogeneous group and should perhaps be limited to *E. tetragona*, *E. odontocarpa*, *E. erythrocorys*, *E. eudesmioides*, and perhaps *E. tetrodonta*. The similarity in form and indumentum of the juvenile leaves, the similarity in appearance and venation of the adult leaves, the tendency to produce flowers on the older parts of the twigs, the several-flowered umbels, the absence of distinct sepaline teeth on the more or less striate or ridged calyx-tube suggest that *E. similis*, *E. baileyana* (and presumably *E. lirata*), *E. phoenicea*, and *E. miniata* are better grouped together in spite of the deeply included valves to the thicker-walled fruits of the two last-mentioned.

It would appear from the diversity of species in Tertiary time and the present occurrence of closely allied species growing in juxtaposition over large areas that speciation in *Eucalyptus* was not dependent on geographical isolation of population segments. Chiefly from a study of the species in south-eastern Australia, Cambage (1913) came to the conclusion that speciation was the direct result of climate and soil composition, a generalization extended by Andrews (1913) to the whole genus. Neither paid any serious attention to the peculiar forms in northern Australia, and some of Andrews' conclusions appear to be quite untenable. There may be sufficient grounds for accepting the general thesis that considerable climatic sorting of species has taken place and that migrations of species from north to south and south to north occurred consequent upon the climatic fluctuations during Pleistocene and Recent times. Herbert (1929) discussed the effect of climate on the distribution of *Eucalyptus* and reviewed earlier work.

These rapid and violent changes in climate must have been of particular importance in the south-eastern part of the continent. Even before the Pleistocene the calcareous nature of the Nullarbor Plain interposed an edaphic barrier between the eastern and western parts of southern Australia, a barrier that was strengthened and extended by the arid conditions of Recent time and the present day. This barrier probably accounts for much of the endemism in south-western Australia.

The northern part of the continent has been much less influenced by these factors and there seems to have been no serious barrier to migration. Old species have had the time and opportunity to become established over large areas. Subsequent climatic changes and earth movements appear to have affected the habitat, largely by the erosion of the substrate, producing the discontinuous distribution shown by many species and exemplified in an extreme case by *Eucalyptus jensenii* (map 27), *E. aspera* (map 4*B*), *E. herbertiana* (map 23*A*), and *E. alba* (map 19). Several wide-ranging species that normally occupy low-lying ground towards the northern (wetter) part of their range are now found on hillsides towards the southern (drier) limit; among these are *E. terminalis, E. papuana, E. alba,* and *E. argillacea* (cf. the distribution of the patches of monsoon forest discussed earlier). Such species as *E. apodophylla, E. abbreviata,* and *E. nesophila* which apparently occupy very restricted areas and are sharply distinct from any allied species, appear to be relict species. In some such cases, the species and those most closely resembling them occupy widely distant areas, e.g. *E. apodophylla* and *E. houseana* (map 22), *E. nesophila* and *E. trachyphloia* (maps 7*A* and 14*C*), and *E. jensenii* and the ironbarks from eastern Queensland discussed in the earlier part of this paper.

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* An apparently endemic species allied to *E. tereticornis* is now known to occur in southern New Guinea. Another species occurs in New Britain and in northern New Guinea extending westward through the Moluccas to Mindanao. This is *E. deglupta* Bl., with which *E. naudiniana* F. Muell. and *E. schlechteri* Diels must be considered conspecific. It seems to be only loosely allied to the Australian species.

Somewhat diverse as have been the ideas about the origin of the genus, it seems to have been generally accepted that it arose in the northern part of Australia with a relatively warm climate. The present preponderance of species in the north with versatile anthers with parallel cells opening in longitudinal slits (sect. *Macrantherae**) and the preponderance in the south of species with other, presumably derived types of anthers, is offered as one point of evidence. Thus, the *Porantheroideae* (species with anthers attached to the filament at or near the base with short, often diverging cells opening in pores) were supposed to have originated in the south and migrated to the north. Andrews claimed that these different groups arose independently of each other and suggested treating them as distinct genera. However, the *Porantheroideae* (series *Buxeales* and *Siderophloiae*) are much more numerous in the north than Andrews supposed (about half the known number of species, of which the majority is not found in the south), and they are much less sharply distinct from the *Macrantherae* than he claimed. For instance, *E. argillacea* has anthers with relatively long anther cells opening in slits and closely veined leaves, both features reminiscent of the *Corymbosae*, but the basal attachment of the anthers, and the fruits and seeds are quite those of the *Buxeales*.

Further, if the *Porantheroideae* arose in the south and migrated north, the migration must have been early enough to allow both the *Buxeales* and *Siderophloiae* to become widely spread in the north, to allow the evolution of the rather numerous endemic species, and to allow time and opportunity for the relict type of distribution exemplified by *E. jensenii.* Such a migration (irrespective of its origin) may account for the variation found in *E. microtheca.* This species is widely spread and abundant on alluvial plains subject to flooding. As understood in this paper, it is a rather variable species to which several names have been given, but as shown previously there seems to be no correlation between the variation in the different characters. It might be supposed that the prototype of such a species could have arisen on the extensive alluvial plains of the pre-arid phase and to have become widely spread. Increasing aridity may have forced it to the stream banks, and it is not inconceivable that the population may have split into two or more isolated segments during the extremes of aridity and then later come into contact again. Under such conditions it is possible that a certain amount of differentiation may have occurred, to become more or less obliterated by later opportunities for gene-flow. The effect of the much more recent decrease in rainfall is probably exemplified by the stunted and shrubby plants more or less corresponding to the form described as *E. coolabah* var. *arida* now found in the desert scrub where there are neither alluvial flats nor watercourses. At Frewena, they occupy the area along which the Frew River once flowed but is now a sanded shallow depression.

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* These sectional names are those used by Blakely; they are not necessarily the correct ones (see under "Subdivisions of the Genus" in the early part of this paper).

At the present time, the geographical range of *E. microtheca* overlaps that of the closely allied *E. tectifica* in the north and *E. largiflorens* to the south and south-east, and trees of *E. microtheca* are sometimes found in close proximity to the species mentioned. Some field observations in Queensland strongly suggest that species of the *Buxeales* and *Siderophloiae* frequently hybridize with one another; it is possible that the general population of *E. microtheca* may be contamined by genes from *E. tectifica* in the north, *E. largiflorens* in the south, and possibly other species as well. Another possibility is that the southern form distinguished as *E. coolabah* by Blakely and Jacobs may indeed be specifically distinct from the northern form to which the name *E. microtheca* was originally applied, and that much the greater part of the area of distribution shown on map 24 may be occupied by a complex hybrid population between these and other species resulting from the migrations just mentioned.

The presence of the Gulf of Carpentaria, formed during Pliocene or Pleistocene time (Whitehouse, personal communication 1950), probably accounts for the apparent division of the distribution areas of *E. tetrodonta* and *E. alba* (maps 17 and 19). I have traversed a considerable portion of the country adjacent to the south-eastern and eastern shores of the Gulf of Carpentaria and believe that the dot on the map at Normanton (the extreme south-eastern corner of the gulf) represents the southern limit of *E. tetrodonta*, and this as an outpost. Other isolated patches on suitable habitats may still await discovery in the area. The rainfall here is much lower than in those places where *E. alba* has been found, and thus a climatic barrier may now prevent a continuous distribution around the shores of the gulf.

The vast extent of the clay soils of the Barkly Tableland also interposes an edaphic barrier that has undoubtedly affected the distribution of many species. Scattered over this extensive plain are remnants of the earlier lateritic cover, and on these *E. pruinosa* is usually present, sometimes as a solitary tree. The intervening heavy soils, like those of the great extent of grasslands in western Queensland, are a formidable barrier to woody plants; they support very few trees (Blake 1938), eucalypts being restricted to *E. microtheca* over the greater part, and then only on and near the banks of watercourses.

Many other problems of distribution are to be met with, but more intensive exploration in the lesser-known areas is required before they can be satisfactorily discussed.

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EXPLANATION OF PLATES 1-36

PLATE 1

Leafless or nearly leafless trees of deciduous species of *Eucalyptus.*

Fig. 1.—*E. tectifica* with grey bark (as at extreme right) and *E. alba* with smooth pale-coloured bark (as in middle) on hillside near Katherine with dense ground cover of dead plants of a tall annual species of *Sorghum;* cf. Plate 2, Figure 2. The small, very dark tree at extreme left is *Petalostigma quadriloculare.*

Fig. 2.—*E. latifolia* (tall trees towards the left) and *E. grandifolia* (white-barked trees towards the right); some *E. tectifica* in the background; cf. Plate 2, Figure 1, and Plate 8. Trees of other genera also present. Gentle slope near Jim Jim Creek, between Pine Creek and Oenpelli (Photos: C. S. Christian).

PLATE 2

Fig. 1.—Crown of flowering tree of *E. grandifolia;* note sparse crown, rigid twigs, smooth, white bark, and tendency for flowers to be borne on leafless twigs. Near "Tipperary" homestead.

Fig. 2.—Predominantly *E. tectifica;* at *a*, *E. patellaris; b*, *E. tetrodonta; c*, young and old trees of *E. foelscheana.* Hard flat S. of Pine Creek. Cf. Plate 1, Figure 1.

Fig. 3.—*E. apodophylla*, partly leafless (*Blake* 17084); occasional tree of *E. latifolia* towards background. Drainage flat E. of junction of McKinlay and Mary Rivers; cf. Plate 3, Figure 1 (Photos: S. T. Blake).

PLATE 3

Fig. 1.—*E. apodophylla* in full leaf; cf. *Blake* 16346 and Plate 2, Figure 3. Flat drainage channel near Brocks Creek.

Fig. 2.—*E. papuana.* Drainage channel near Brocks Creek (Photos: C. S. Christian).

PLATE 4

Fig. 1.—*E. miniata* (as at left and centre, *Blake* 16220 was collected in the vicinity), and *E. confertiflora* (as at extreme right, *Blake* 16236; see also Plate 5, Figure 2). S. of Brocks Creek.

Fig. 2.—*E. foelscheana* (*Blake* 16108). Brocks Creek. See also Plate 5, Figure 1 (Photos: C. S. Christian).

PLATE 5

Upper parts of trunks of *E. foelscheana* (Fig. 1) and *E. confertiflora* (Fig. 2), showing persistent, tessellated, or scaly bark on lower part and smooth, deciduous, light-coloured bark on the upper part in the act of decorticating in large, thin flakes. Near Brocks Creek (Photos: C. S. Christian).

PLATE 6

Figs. 1 and 2.—*E. setosa;* habit and bark (*Perry* 613), 50 miles N. of Tennant Creek.

Fig. 3.—*E. brevifolia* (*Perry* 2311). "Limbunya" Station.

Fig. 4.—*E. bleeseri* (*Blake* 16380). Near Brocks Creek (Photos: Figs. 1-3, R. A. Perry; Fig. 4, S. T. Blake).

PLATE 7

E. terminalis; habit and bark (*Perry* 2143). SSE. of "Victoria River Downs" Station. (Photos: R. A. Perry.)

PLATE 8

E. latifolia; habit and bark (*Perry* 2706); the transition from scaly bark to smooth bark is shown. ENE. of "Bradshaw" Station (Photos: R. A. Perry).

PLATE 9

E. tetrodonta; type (Photo: W. J. Sanderson).

PLATE 10

E. clavigera; isotype (Photo: W. J. Sanderson).

PLATE 11

E. polysciada; type (Photo: W. J. Sanderson).

PLATE 12

E. abbreviata; isotype (Photo: W. J. Sanderson).

PLATE 13

E. terminalis

Fig. 1.—Best-developed fruit and leaf from holotype of *E. terminalis.*

Fig. 2.—Part of lectotype of *E. pyrophora;* twig with bud, loose leaf, bud, operculum, and flower.

Fig. 3.—Leaf and bud of another syntype of *E. pyrophora.*

Fig. 4.—Fruits, twig with mature buds, and piece of bark from *Blake* 10102; the piece of bark at bottom left was accidentally placed in the horizontal instead of the vertical position. Cf. Plate 7 (Photo: W. J. Sanderson).

PLATE 14

E. polycarpa; type (Photo: W. J. Sanderson).

PLATE 15

E. dichromophloia; lectotype (Photo: W. J. Sanderson).

PLATE 16

E. dichromophloia; part of lectotype of *E. niphophloia* (Photo: W. J. Sanderson).

PLATE 17

E. latifolia; type (Photo: W. J. Sanderson).

PLATE 18

E. foelscheana; syntype collected by McKinlay; cf. Plate 19 (Photo: W. J. Sanderson).

PLATE 19

E. foelscheana; syntype collected by Foelsche; another leaf constitutes a second sheet; cf. Plate 18 (Photo: W. J. Sanderson).

PLATE 20

E. foelscheana; lectotype of *E. leiophloia* (Photo: W. J. Sanderson).

PLATE 21

E. foelscheana; isotype of *E. leiophloïa* var. *lepidophloia* (Photo: W. J. Sanderson).

PLATE 22

E. porrecta

Fig. 1.—Portion of type.

Fig. 2.—Portion of paratype (Photos: W. J. Sanderson).

PLATE 23

E. jacobsiana; isotype (Photo: W. J. Sanderson).

PLATE 24

E. alba

Figs. 1 and 2.—*Teysmann* 7951 (Solor).

Fig. 3.—A leaf from *Teysmann* 7949 (Timor).

Fig. 4.—*Jacobs* 42 (Bathurst Island) (Photo: W. J. Sanderson).

PLATE 25

Fig. 1.—A leaf from an isotype of *E. alba* var. *australasica.*

Figs. 2 and 3.—Portions of paratype of *E. alba* var. *australasica.* See also Plate 30, Figures 1 and 2 (Photo: W. J. Sanderson).

PLATE 26

E. alba; portion of one sheet of *Blake* 16797; see also Plate 30, Figure 3 (Photo: W. J. Sanderson).

PLATE 27

E. alba; type of *E. platyphylla;* see also Plate 30, Figure 10 (Photo: W. J. Sanderson).

PLATE 28

E. alba; portion of lectotype of *E. platyphylla* var. *tintinnans;* details of bud shown in Plate 30, Figure 6 (Photo: W. J. Sanderson).

PLATE 29

E. alba; Specht 575A; note variation in leaf shape; details of buds and fruit shown in Plate 30, Figure 8 (Photo: W. J. Sanderson).

PLATE 30

Buds and fruits of *Eucalyptus* spp. Figs. 1-18.—*E. alba;* Fig. 19.—*E. bigalerita;* Figs. 20-36.—*E. microtheca;* Figs. 37-41.—*E. oligantha.*

Fig. 1.—*Jacobs* 48 (lectotype of *E. alba* var. *australasica*); 2, *Jacobs* 46 (paratype of *E. alba* var. *australasica*); 3, *Blake* 16797; 4, *Blake* 17083; 5, *Jensen* 404; 6, *Jacobs* 77 (lectotype of *E. platyphylla* var. *tintinnans*); 7, *Jacobs* 89; 8, *Specht 575A;* 9, *Specht* 1216; 10, Burdekin, *Mueller* (type of *E. platyphylla*); 11, Charters Towers, *Plant;* 12, Palm Island, *Bancroft;* 13, *Persieh* 4; 14, Timor (*BRI*); 15, *Teysmann* 7946; 16, *Brass* 771; 17, *Teysmann* 7951; 18, *Jacobs* 42; 19, *Blake* 16624; 20, Victoria River, *Mueller* (type collection of *E. microtheca*); 21, *Blake* 17216; 22, *Blake* 17767; 23, *Blake* 17836; 24, *Blake* 17231; 25, *Basedow* 17 (type of *E. coolabah* var. *arida*); 26, *Jacobs* 141 (type of *E. microtheca* var. *cymbaliformis*); 27, *White* 3431; 28, *Blake* 17922; 29, *Beasley* 31; 30, Bourke, *Maiden* (topotype of *E. coolabah*); 31, *Perry* 809; 32, *Blake* 17971; 33, *Blake* 5346; 34, *Perry* 728; 35, *Perry* 868; 36, *Blake* 17882; 37, *Blake* 16991; 38, *Blake* 17179; 39, *Jacobs* 58 (type of *E. hillii* var. *alleniana*); 40, *Blake* 16221; 41, *Jacobs* 41 (Photo: W. J. Sanderson).

PLATE 31

E. bigalerita, type (Photo: W. J. Sanderson).

PLATE 32

E. oligantha

Fig. 1.—From type of *E. hillii.*

Fig. 2.—*Jacobs* 41 from the type locality of *E. hillii;* see also Plate 30, Figure 41.

Fig. 3.—Isotype of *E. hillii* var. *alleniana;* fruits shown in Plate 30, Figure 39 (Photo: W. J. Sanderson).

PLATE 33

E. oligantha; part of one sheet of *Blake* 16991 (see also Plate 30, Figure 37) (Photo: W. J. Sanderson).

PLATE 34

E. microtheca; part of type (?); see also Plate 30, Figure 20 (Photo: W. J. Sanderson).

PLATE 35

E. cyanoclada; type (Photo: W. J. Sanderson).

PLATE 36

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Fig. 1.—Portion of type.

Figs. 2 and 3.—Pieces from *Blake* 12477 (Photo: W. J. Sanderson).

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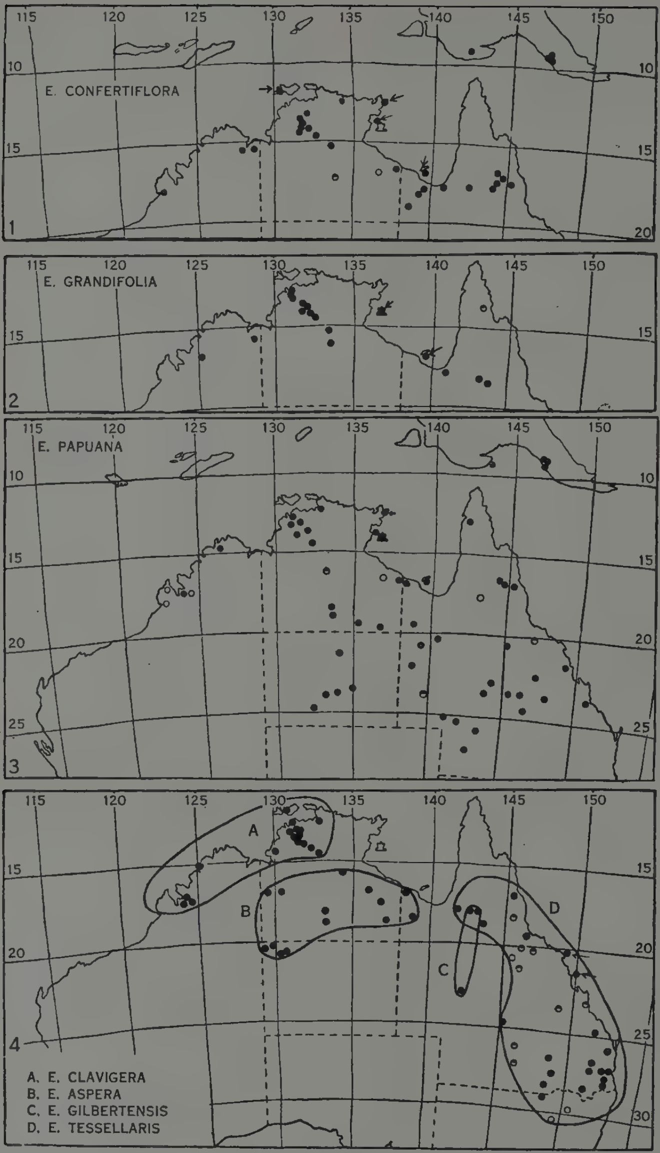
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E. CONFERTIFLORA
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E. GRANDIFOLIA
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A. E. CLAVIGERA
B. E. ASPERA
C. E. GILBERTENSIS
D. E. TESSELLARIS
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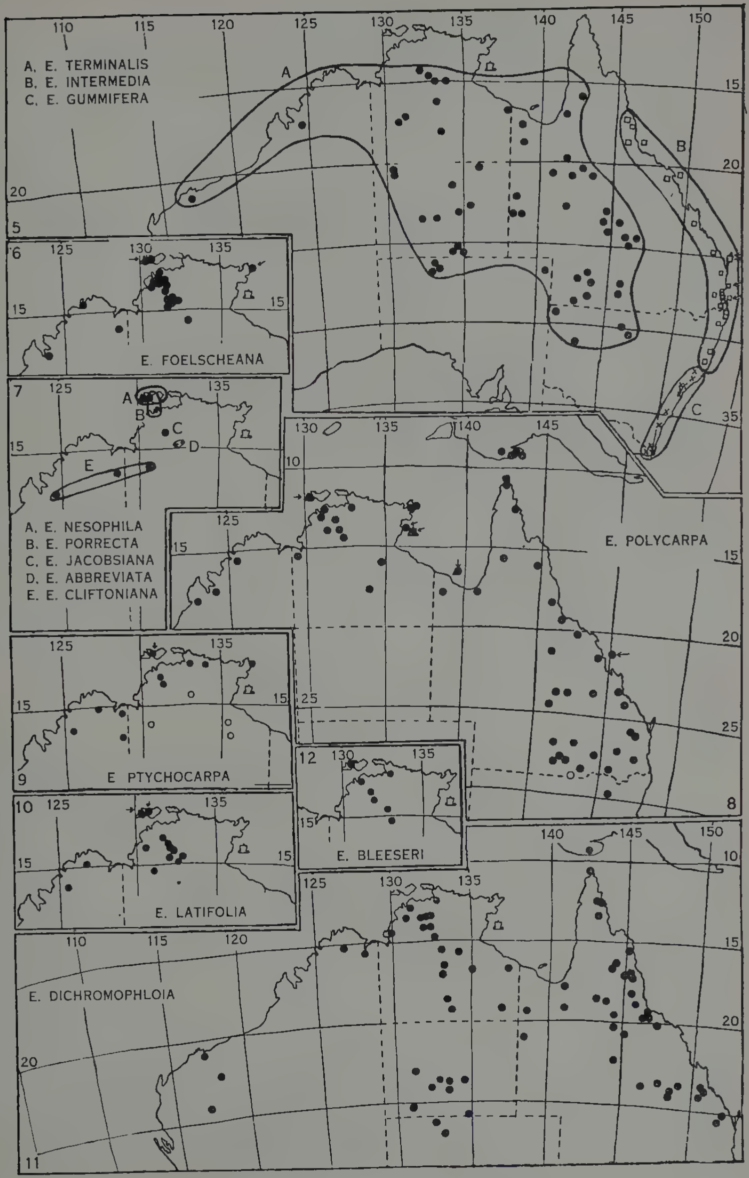
Distribution maps 1-4.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A. E. TERMINALIS
B. E. INTERMEDIA
C. E. GUMMIFERA
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E. FOELSCHEANA
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E
A. E. NESOPHILA
B. E. PORRECTA
C. E. JACOBSIANA
D. E. ABBREVIATA
E. E. CLIFTONIANA
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E. POLYCARPA
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E PTYCHOCARPA
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E. LATIFOLIA
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E. DICHROMOPHLOIA
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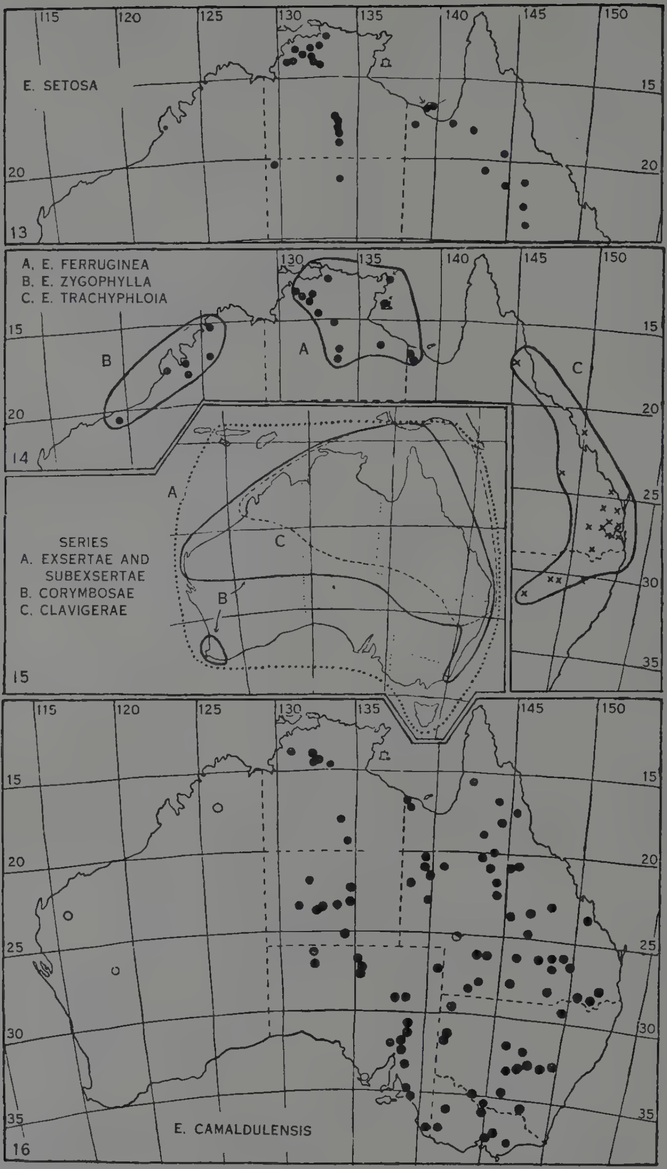
Distribution maps 5-12.


E. SETOSA
13
A. E. FERRUGINEA
B. E. ZYGOPHYLLA
C. E. TRACHYPHLOIA
14
SERIES
A. EXSERTAE AND SUBEXSERTAE
B. CORYMBOSAE
C. CLAVIGERAE
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E. CAMALDULENSIS
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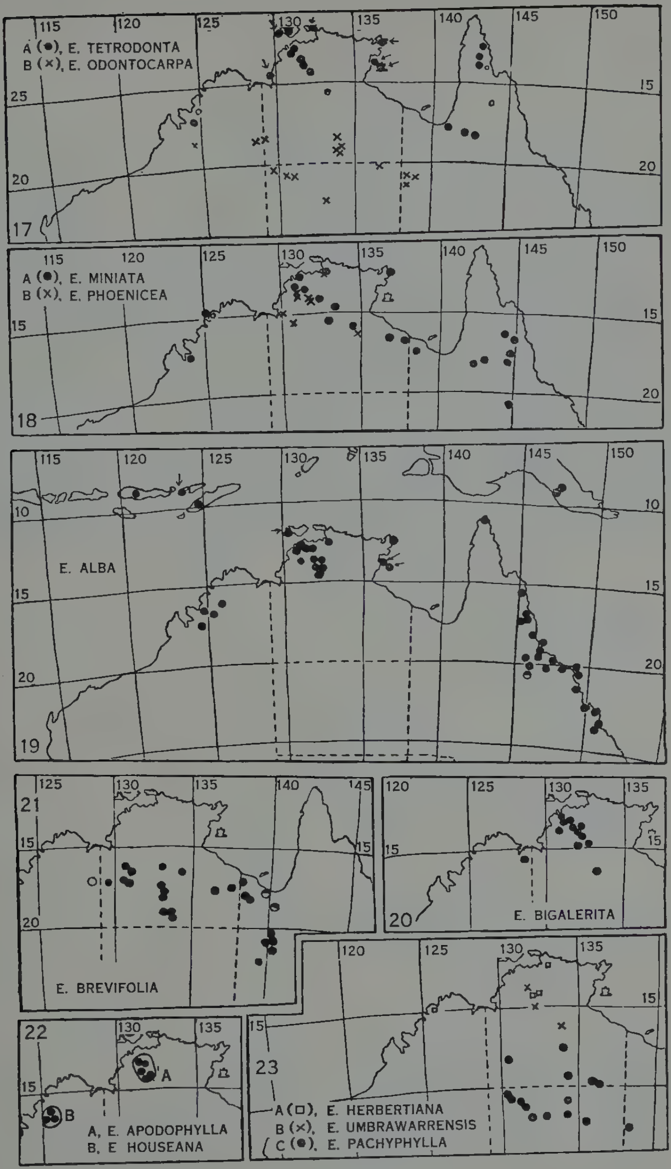
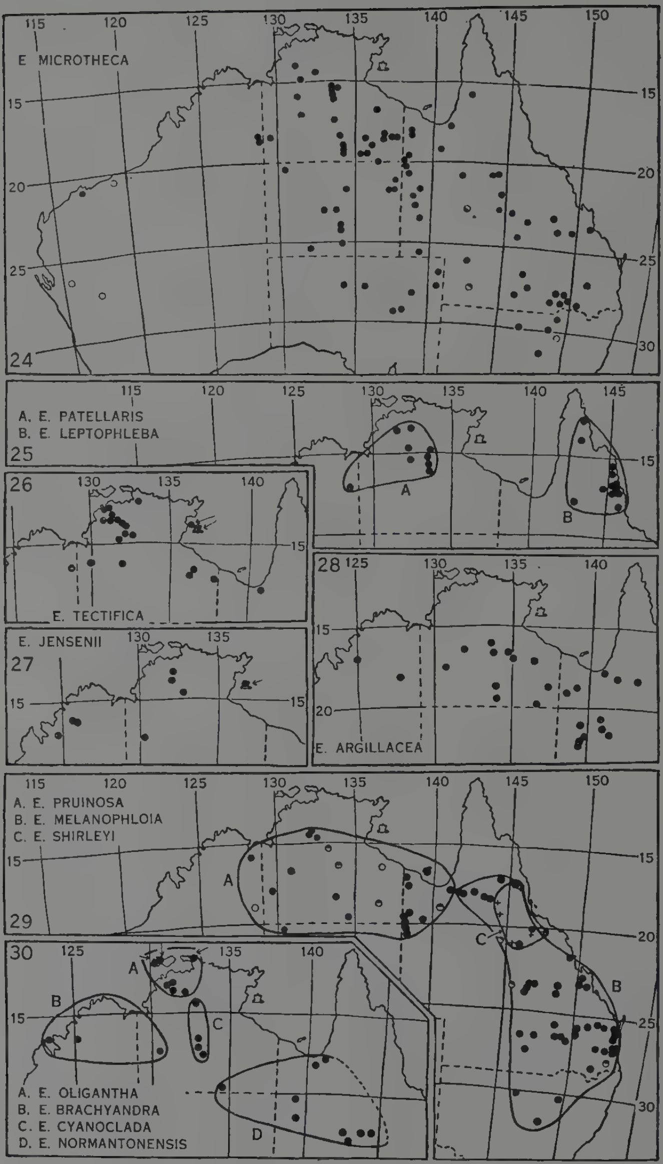
Distribution maps 13-16.


17
A (●), E. TETRODONTA
B (×), E. ODONTOCARPA
18
A (●), E. MINIATA
B (×), E. PHOENICEA
19
E. ALBA
21
E. BREVIFOLIA
20
E. BIGALERITA
22
A, E. APODOPHYLLA
B, E HOUSEANA
23
A (□), E. HERBERTIANA
B (×), E. UMBRAWARRENSIS
C (●), E. PACHYPHYLLA

Distribution maps 17-23.


24
E MICROTHECA
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A. E. PATELLARIS
B. E. LEPTOPHLEBA
26
E. TECTIFICA
27
E. JENSENII
28
E. ARGILLACEA
29
A. E. PRUINOSA
B. E. MELANOPHLOIA
C. E. SHIRLEYI
30
A. E. OLIGANTHA
B. E. BRACHYANDRA
C. E. CYANOCLADA
D. E. NORMANTONENSIS
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Distribution maps 24-30.

NORTHERN AUSTRALIAN SPECIES OF EUCALYPTUS

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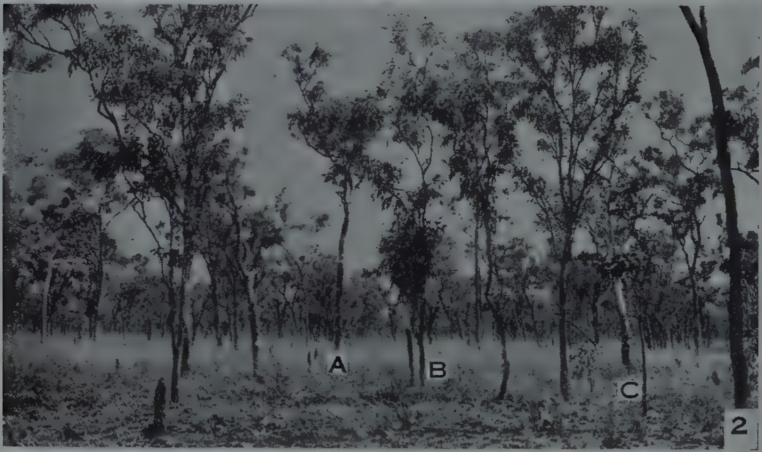

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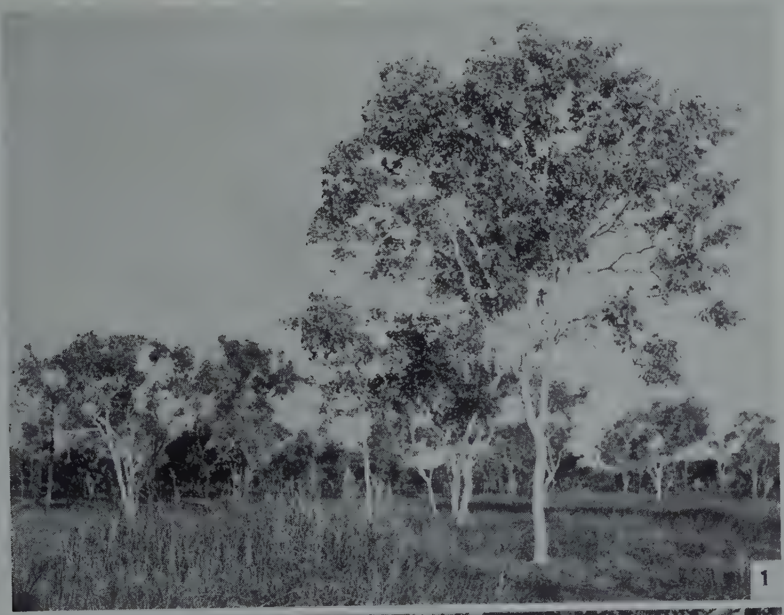
NORTHERN AUSTRALIAN SPECIES OF EUCALYPTUS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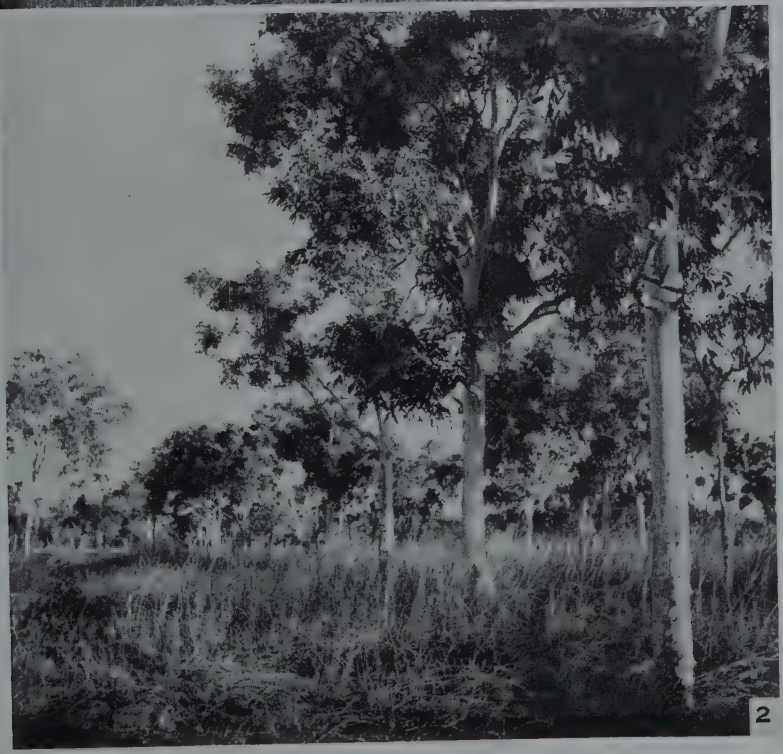
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NORTHERN AUSTRALIAN SPECIES OF EUCALYPTUS

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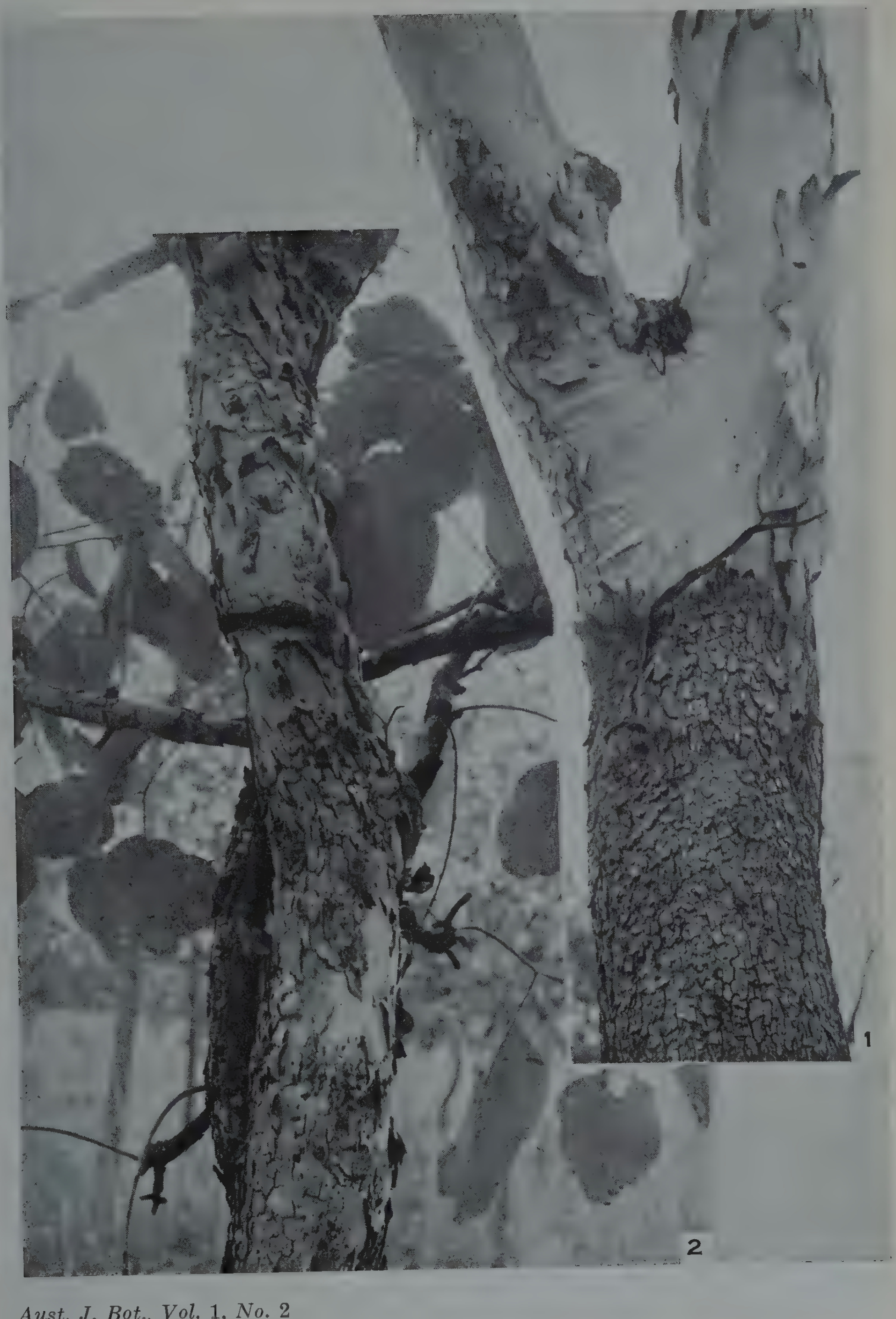
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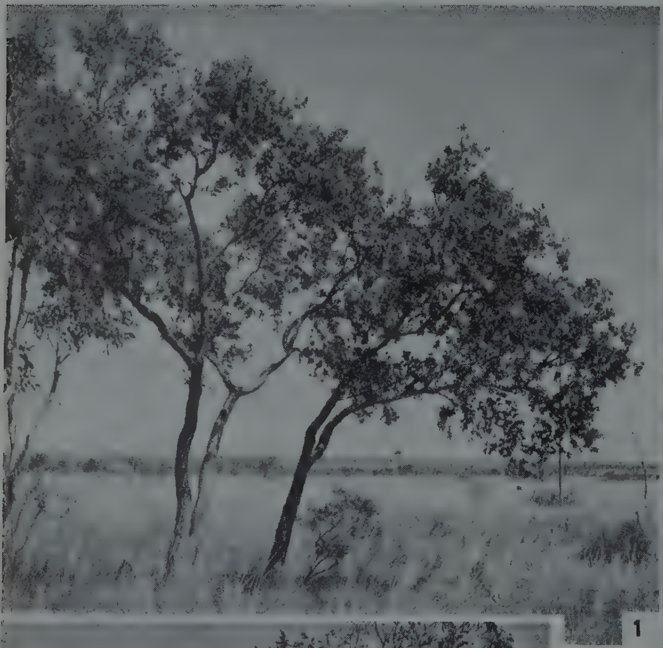
NORTHERN AUSTRALIAN SPECIES OF EUCALYPTUS



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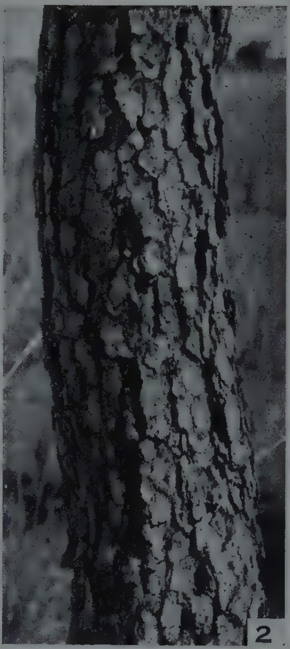

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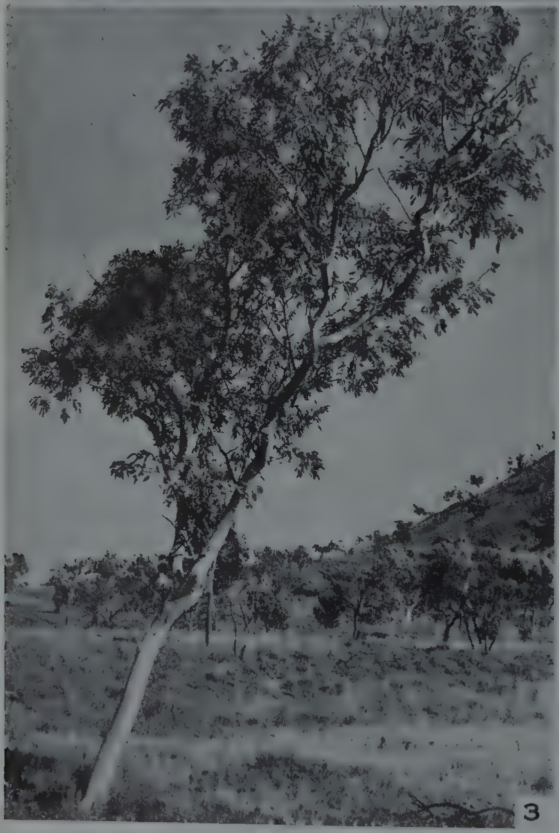

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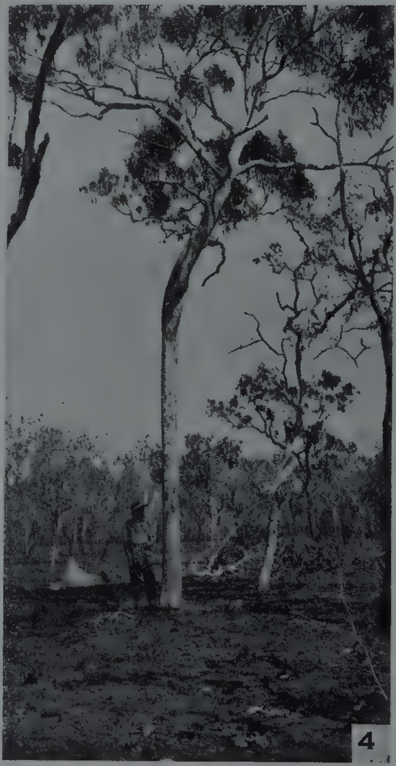

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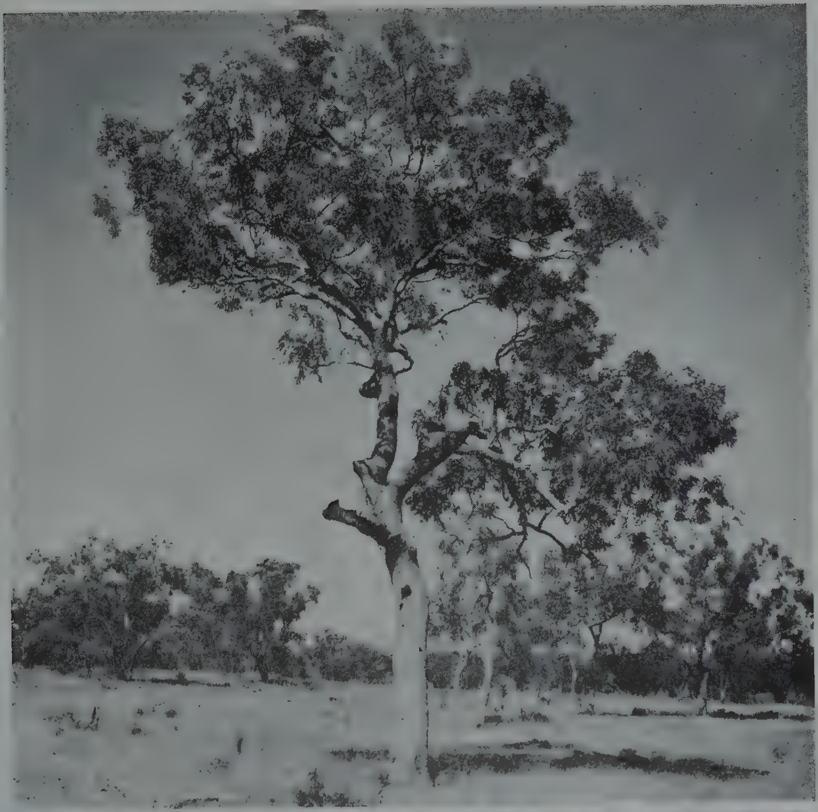
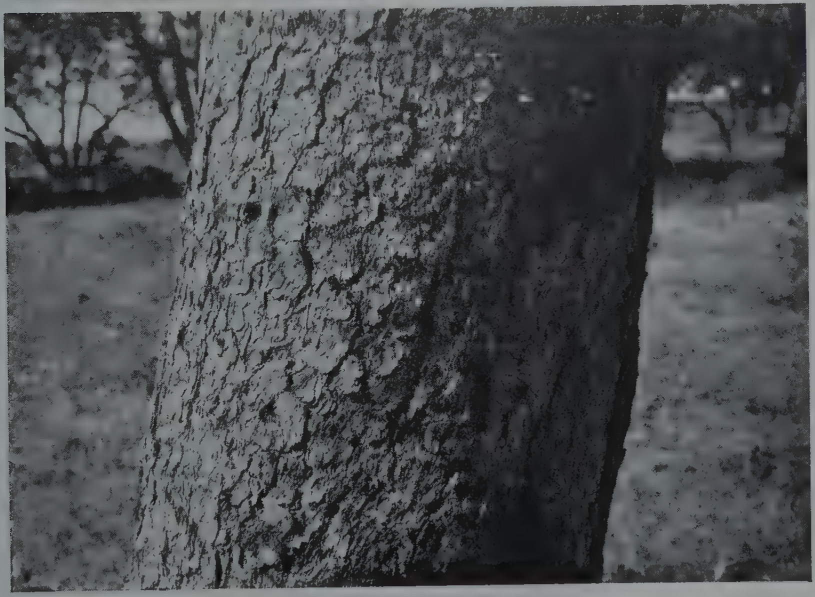
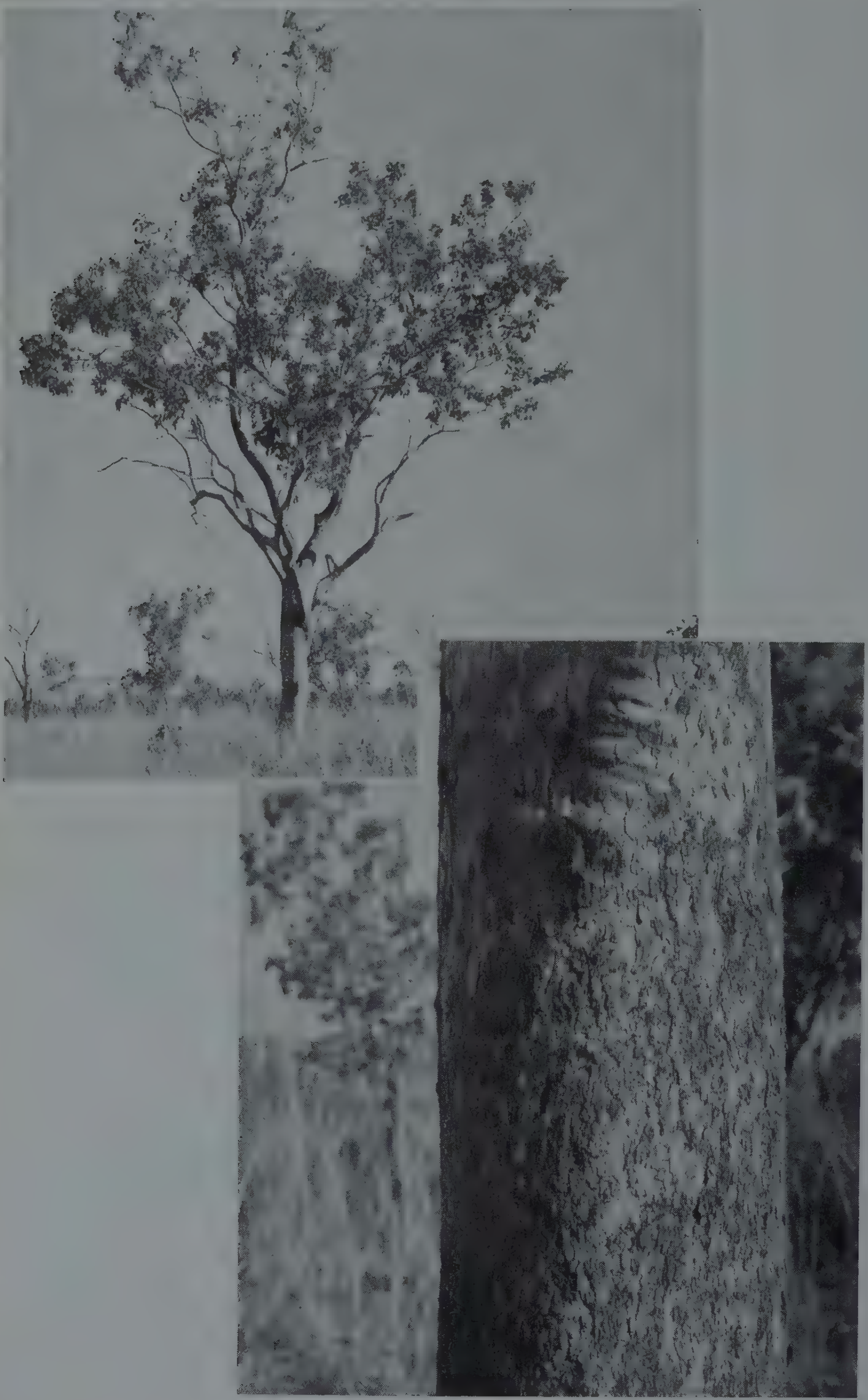
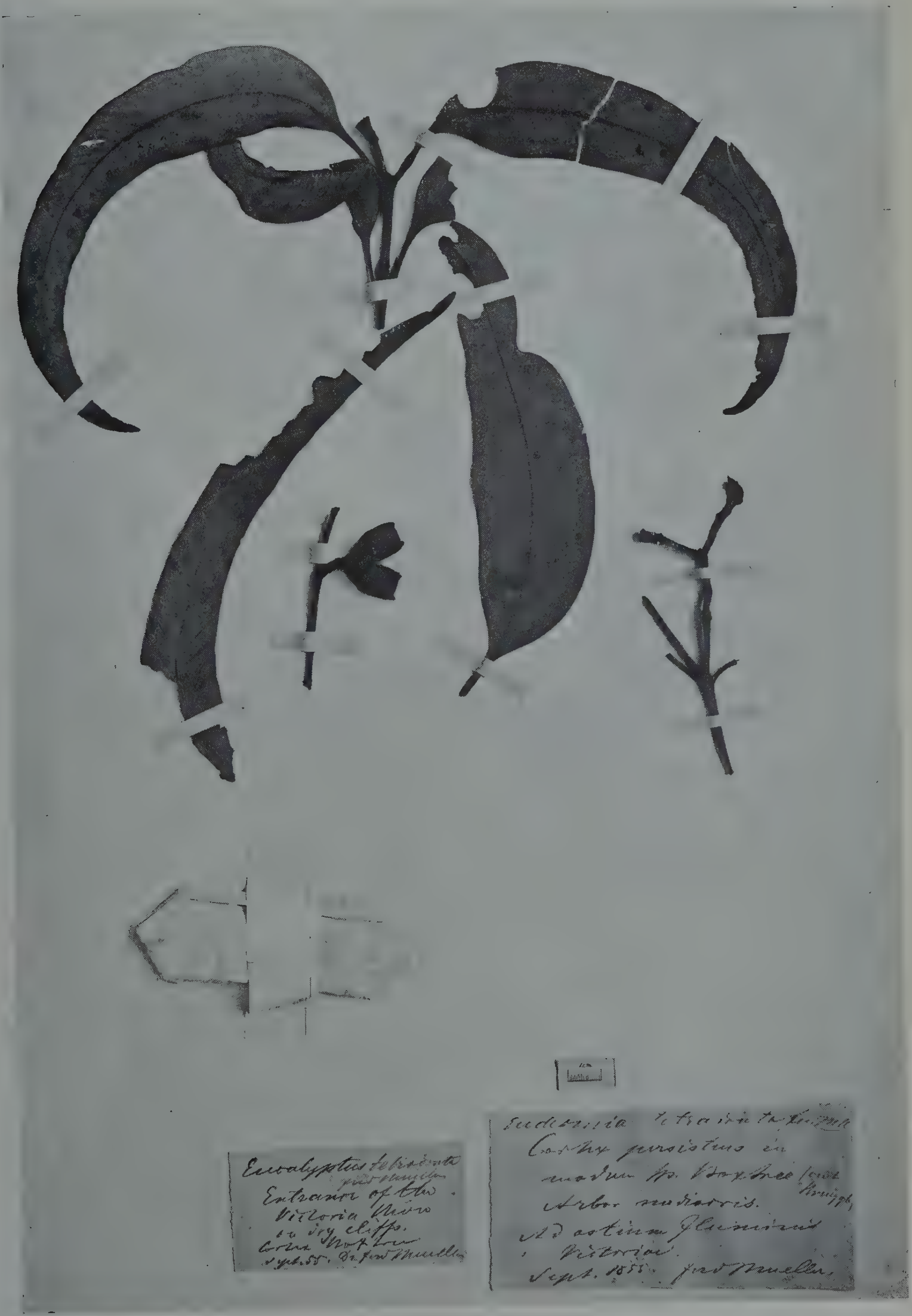
NORTHERN AUSTRALIAN SPECIES OF EUCALYPTUS

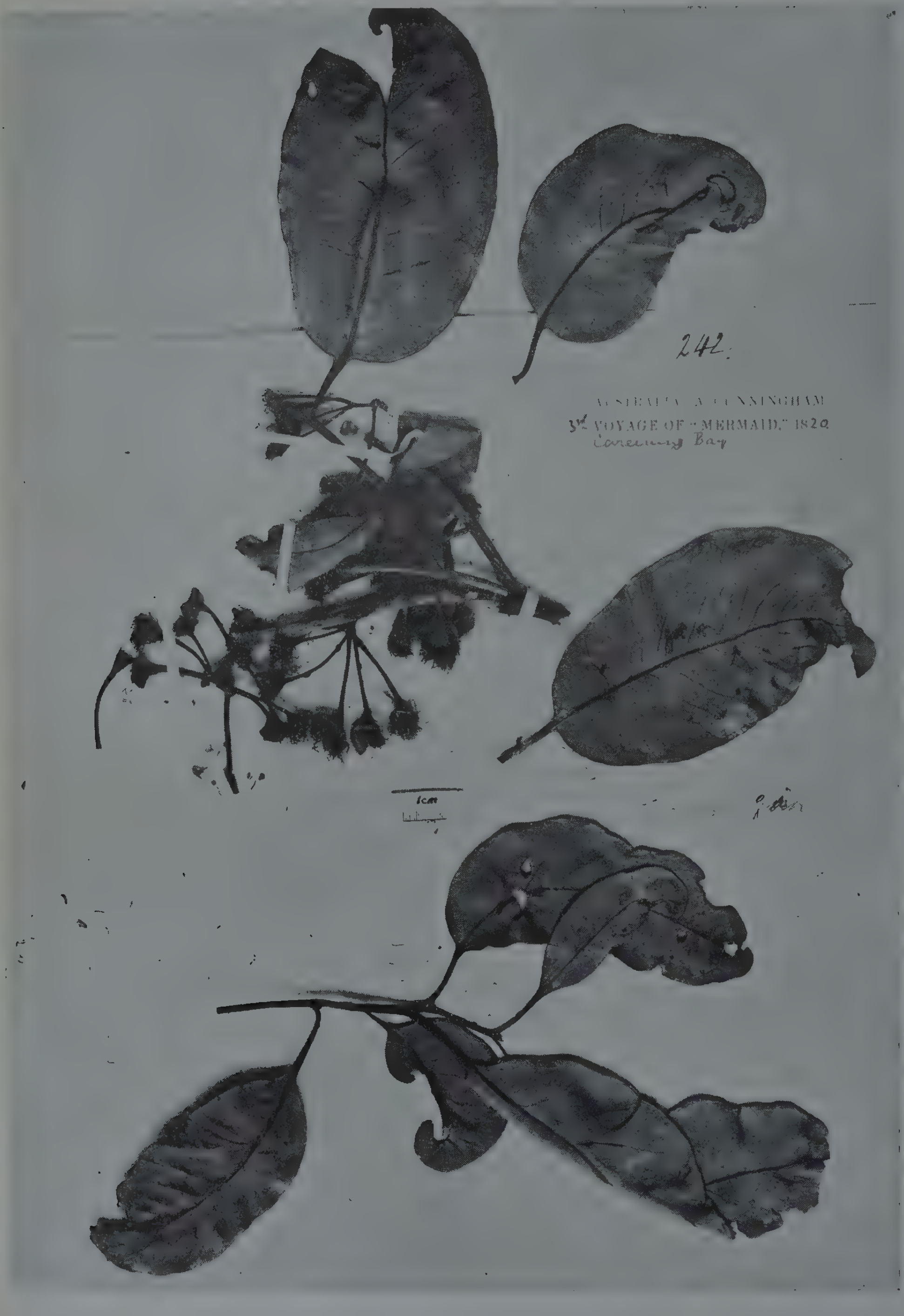


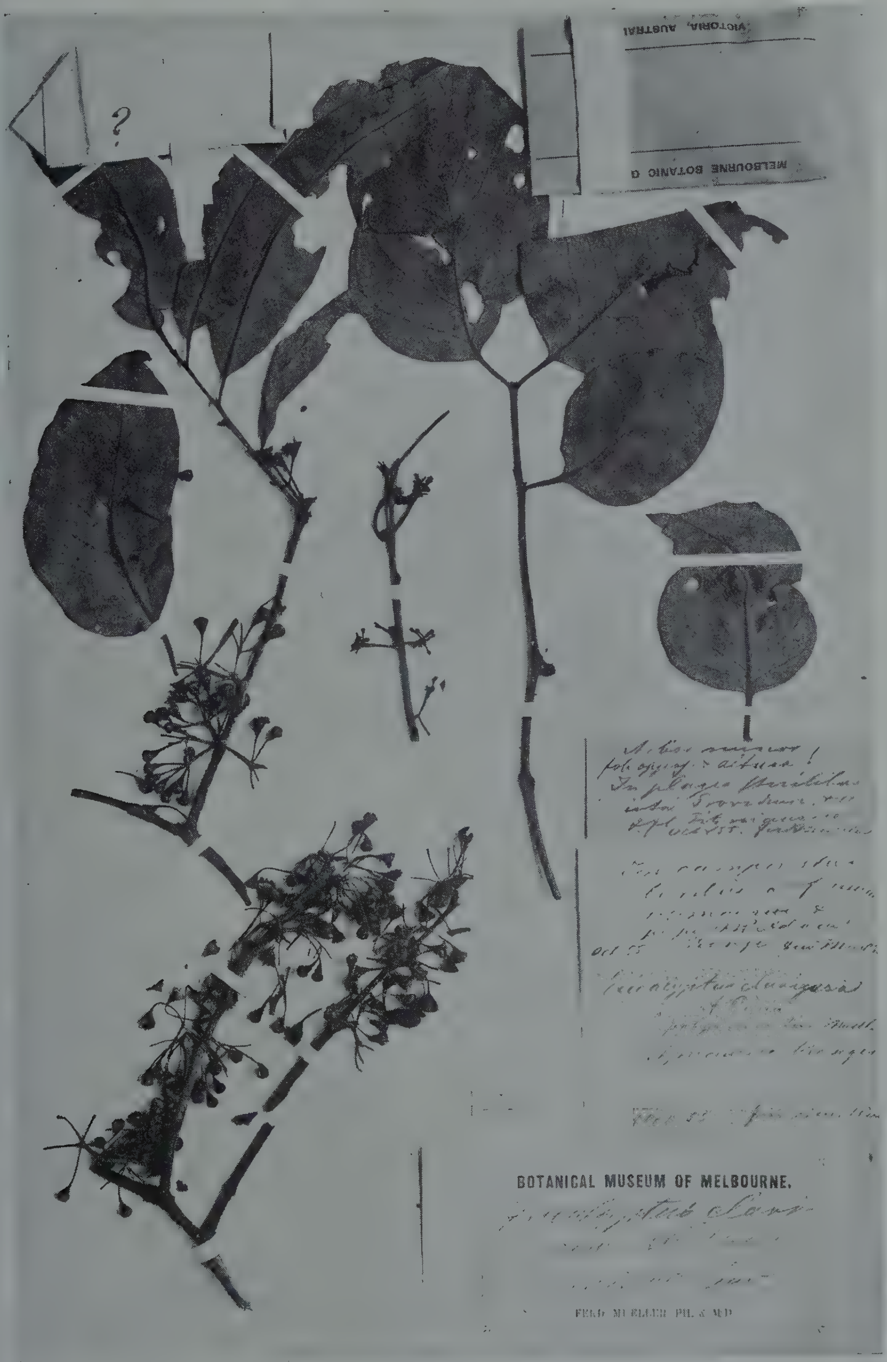




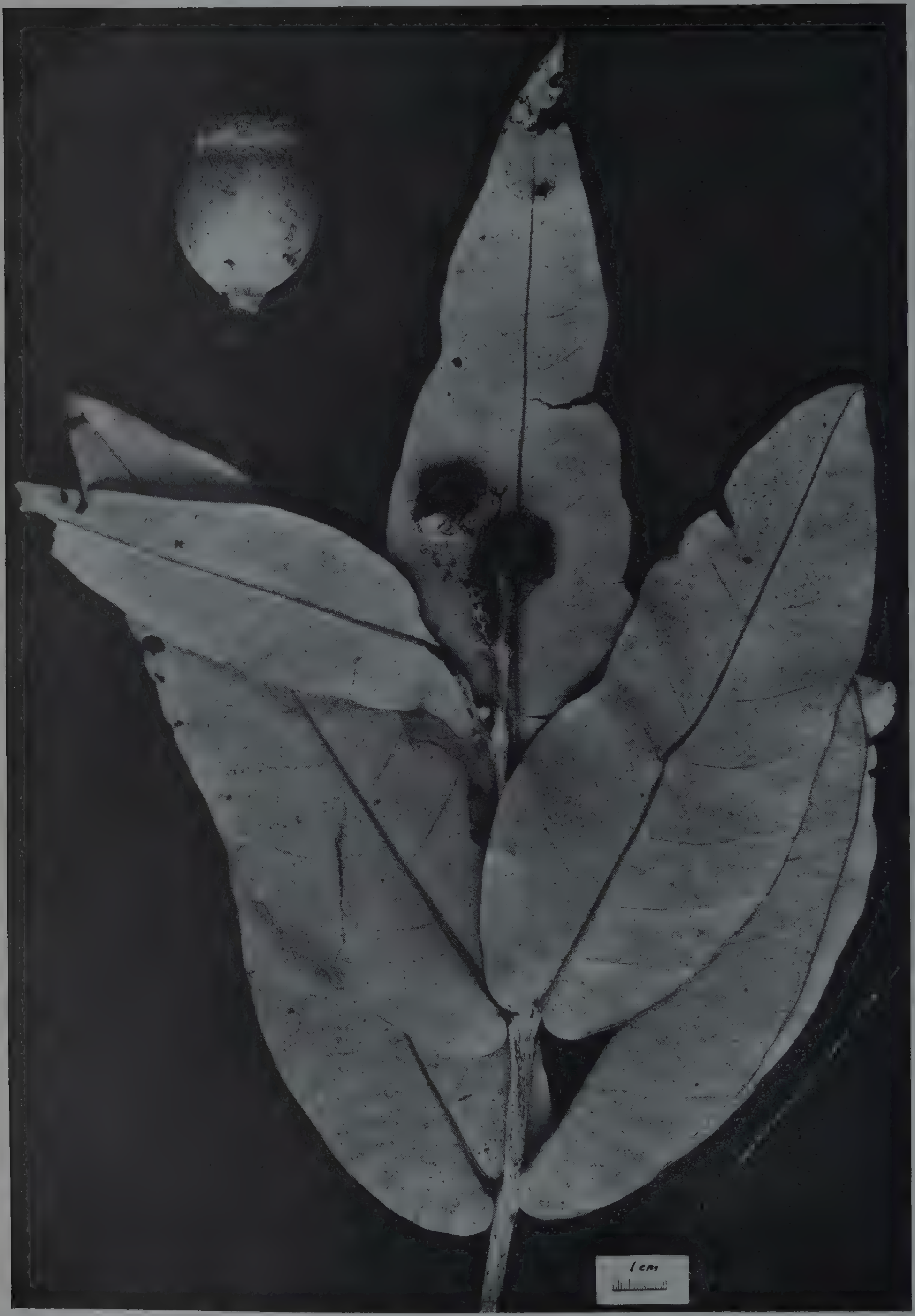
NORTHERN AUSTRALIAN SPECIES OF EUCALYPTUS


1cm
Eucalyptus tetrodonta
F. v. Mueller
Entrance of the
Victoria River
on dry cliffs.
Cortex Stringybark
Sept. 55. Dr Ferd Mueller
Eudesmia tetrodonta F. Muell.
Cortex persistens in
modum Sp. Stringybark (not Ironbark)
Arbor mediocris.
Ad ostium fluminis
Victoriae.
Sept. 1855. Ferd Mueller.

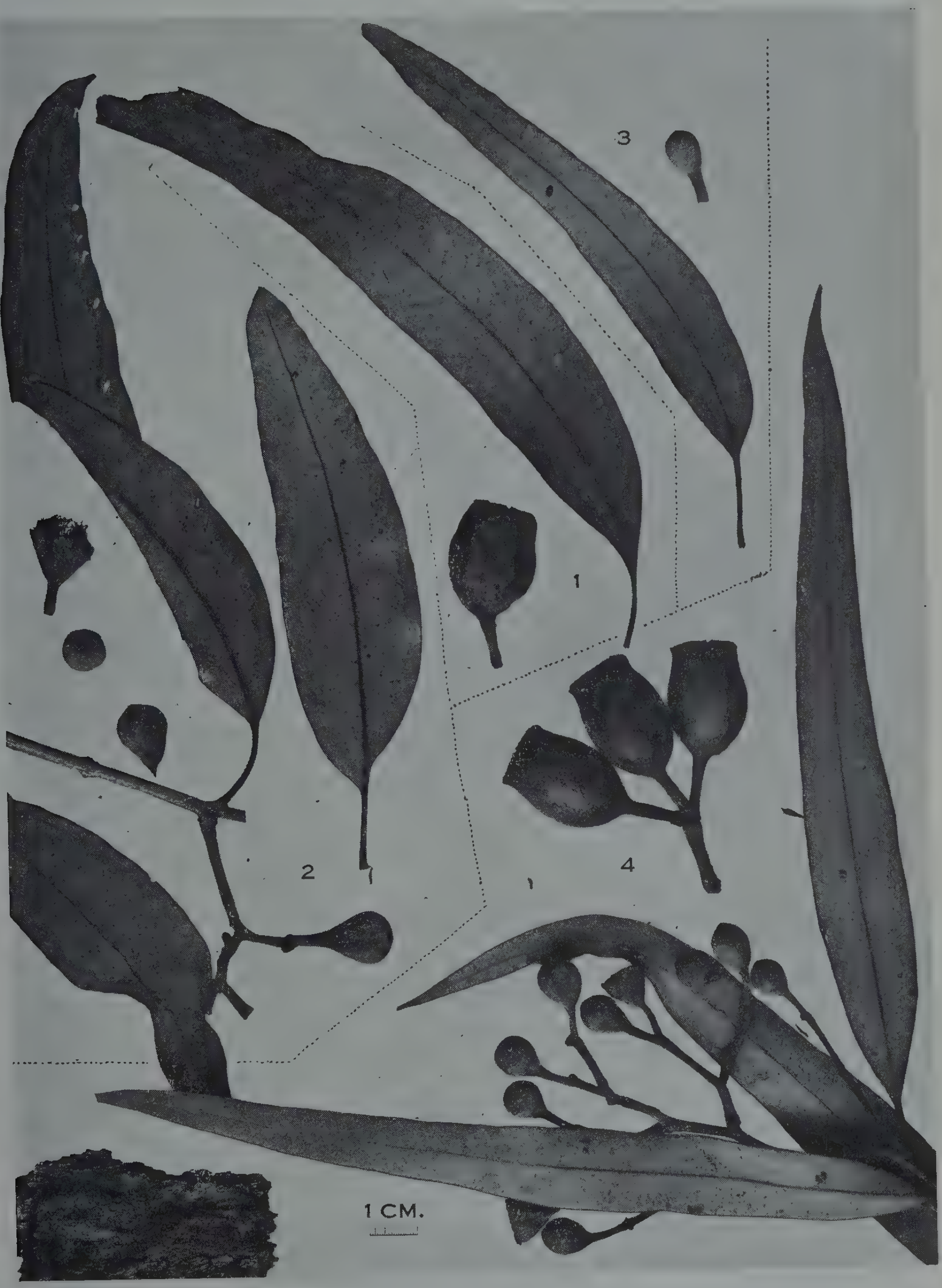

242.
AUSTRALIA A. CUNNINGHAM
3rd VOYAGE OF "MERMAID," 1820
Careening Bay
1cm


?
VICTORIA, AUSTRAL
MELBOURNE BOTANIC G
BOTANICAL MUSEUM OF MELBOURNE.
FERD. MUELLER PH. & M.D.

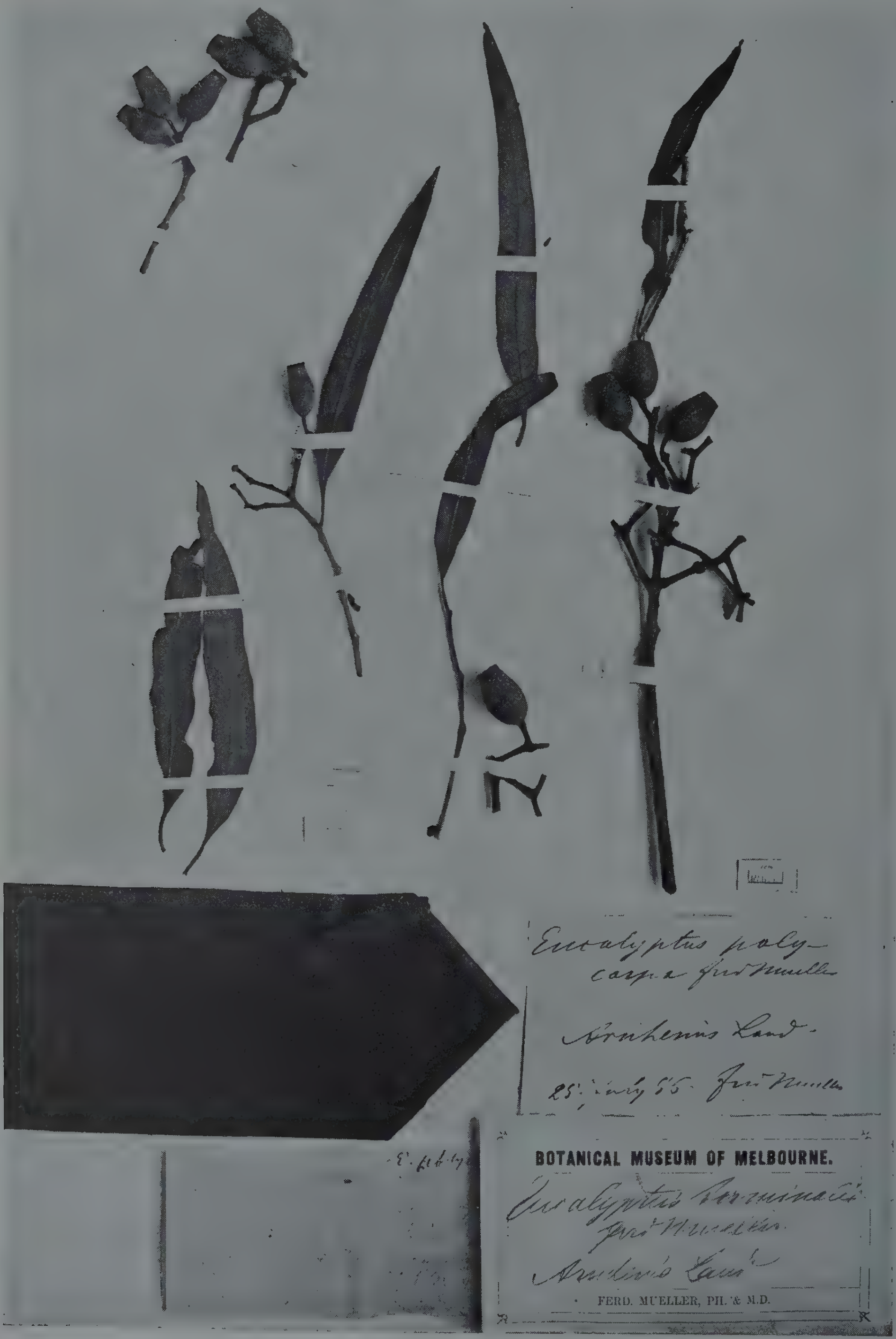
NORTHERN AUSTRALIAN SPECIES OF EUCALYPTUS



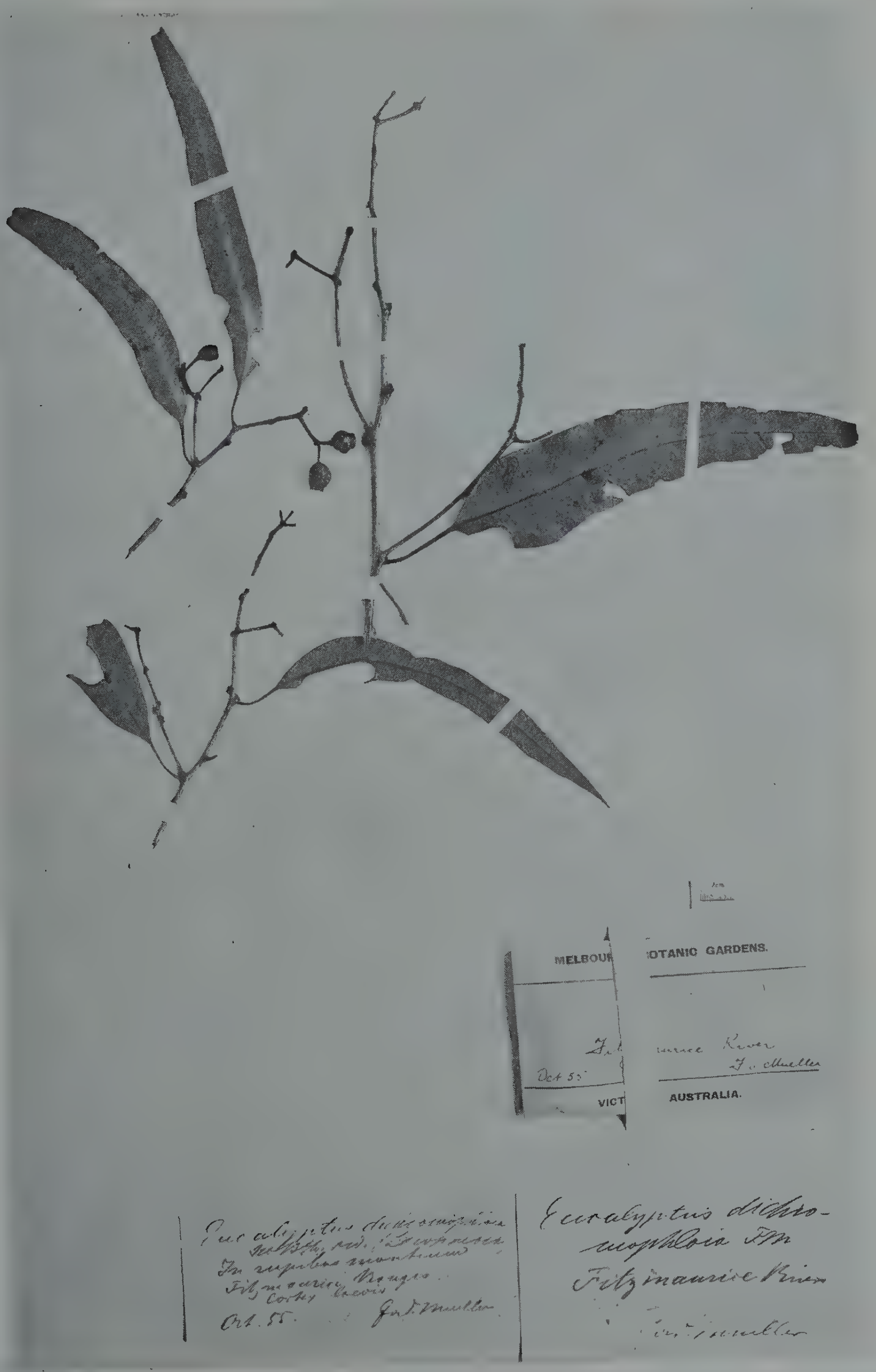
NORTHERN AUSTRALIAN SPECIES OF EUCALYPTUS

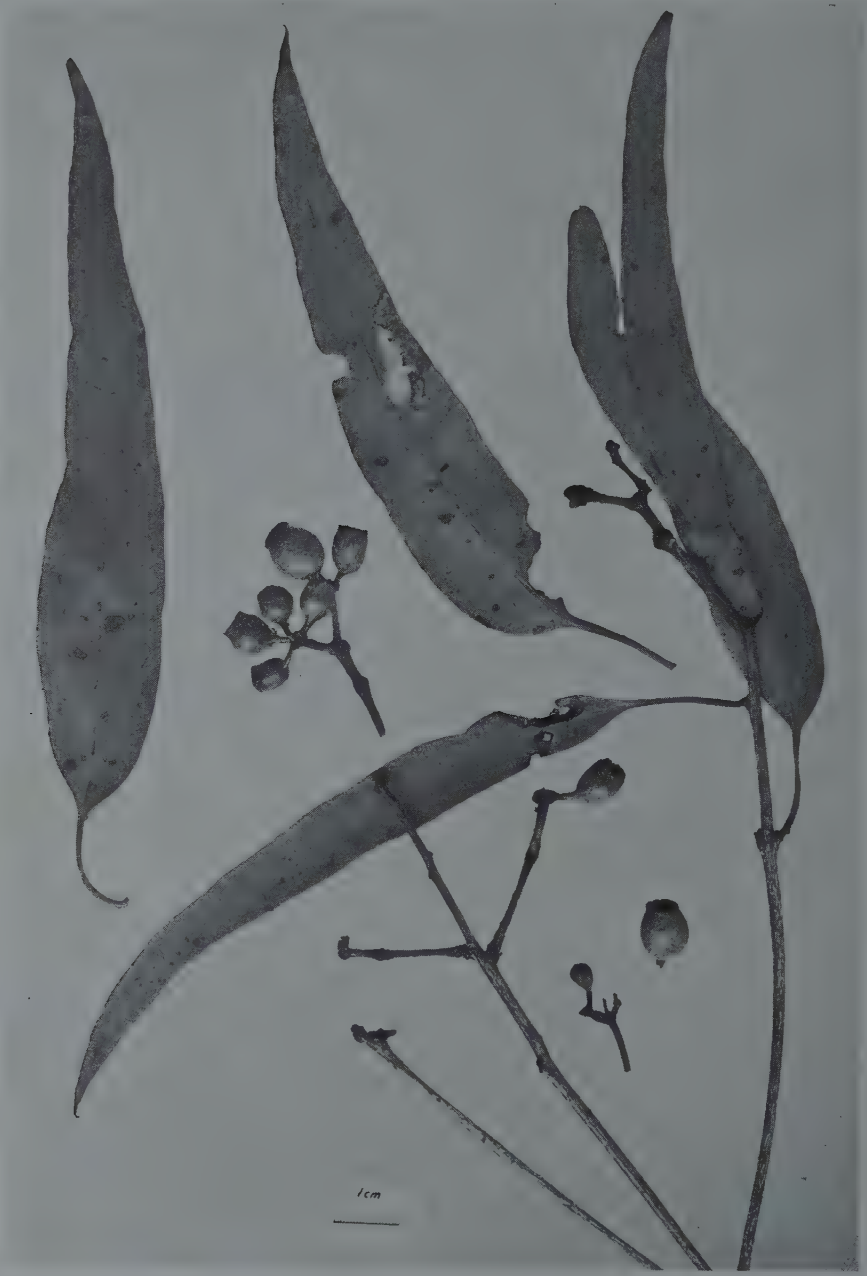


NORTHERN AUSTRALIAN SPECIES OF EUCALYPTUS

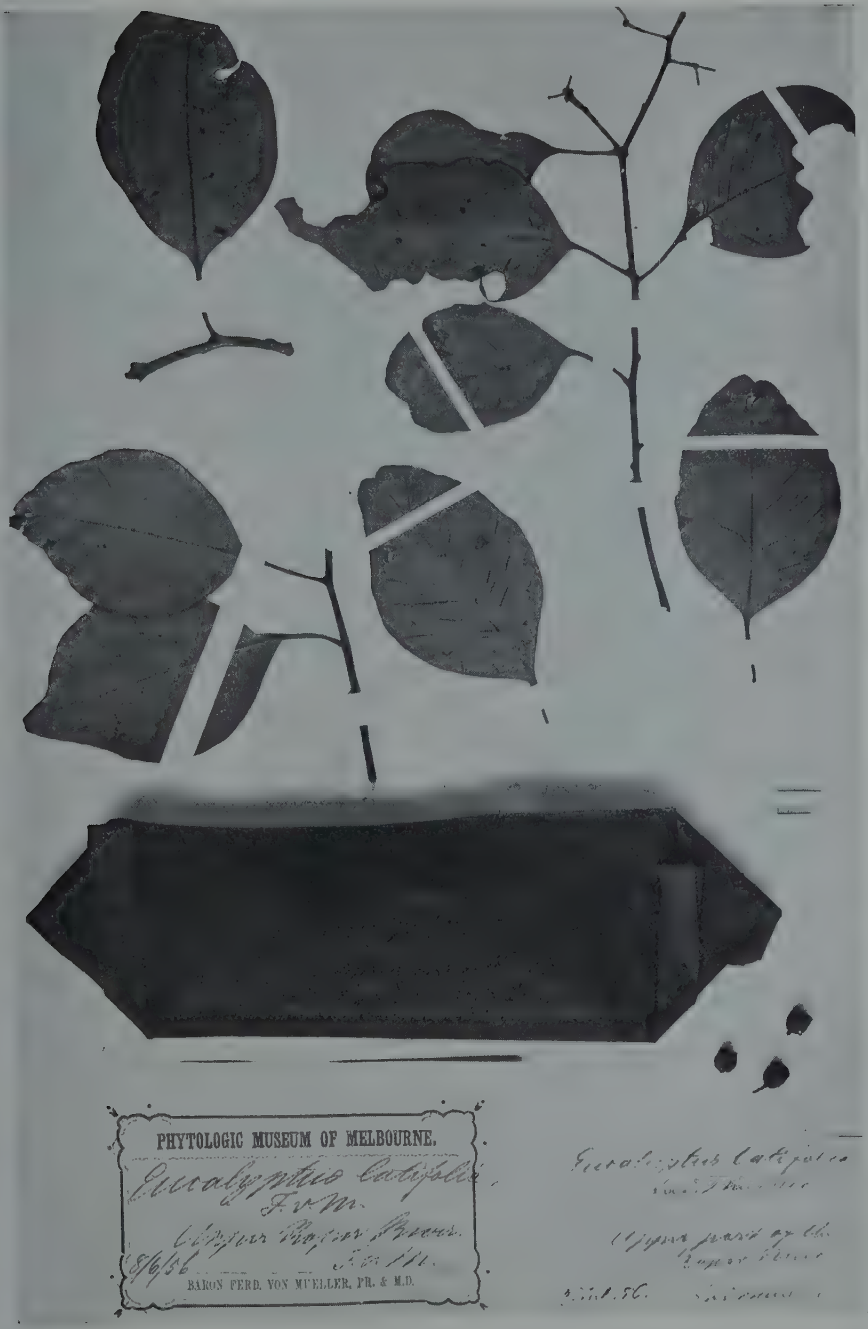

Eucalyptus polycarpa Ferd Mueller
Arnhems Land.
25. July 55. Ferd Mueller
E. polyc
BOTANICAL MUSEUM OF MELBOURNE.
Eucalyptus terminalis Ferd Mueller.
Arnhems Land
FERD. MUELLER, PH. & M.D.

NORTHERN AUSTRALIAN SPECIES OF EUCALYPTUS

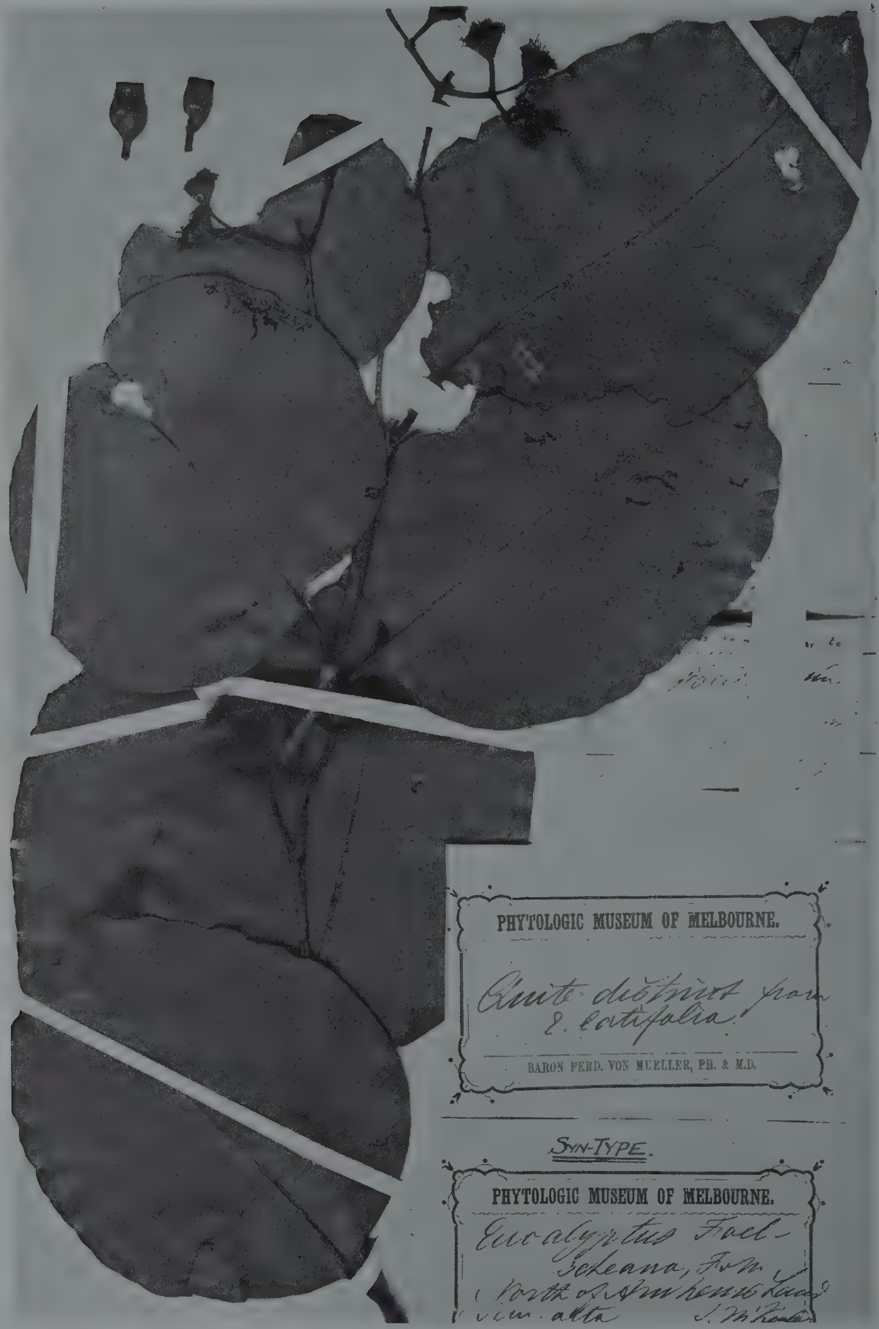

MELBOUR
OTANIC GARDENS.
Fit[illegible] urice River
F. Mueller
Oct 55
VICT
AUSTRALIA.
Eucalyptus dichromophloia
[illegible]
In rupibus montium
Fitzmaurice Ranges.
Cortex laevis
Oct. 55.
Ferd. Mueller
Eucalyptus dichromophloia F.M.
Fitzmaurice River
F. Mueller


1cm

NORTHERN AUSTRALIAN SPECIES OF EUCALYPTUS


PHYTOLOGIC MUSEUM OF MELBOURNE.
Eucalyptus latifolia
F.v.M.
Upper Roper River.
8/6/56
BARON FERD. VON MUELLER, PH. & M.D.
Eucalyptus latifolia
Upper part of the Roper River

NORTHERN AUSTRALIAN SPECIES OF EUCALYPTUS



PHYTOLOGIC MUSEUM OF MELBOURNE.

Quite distinct from
E. latifolia!

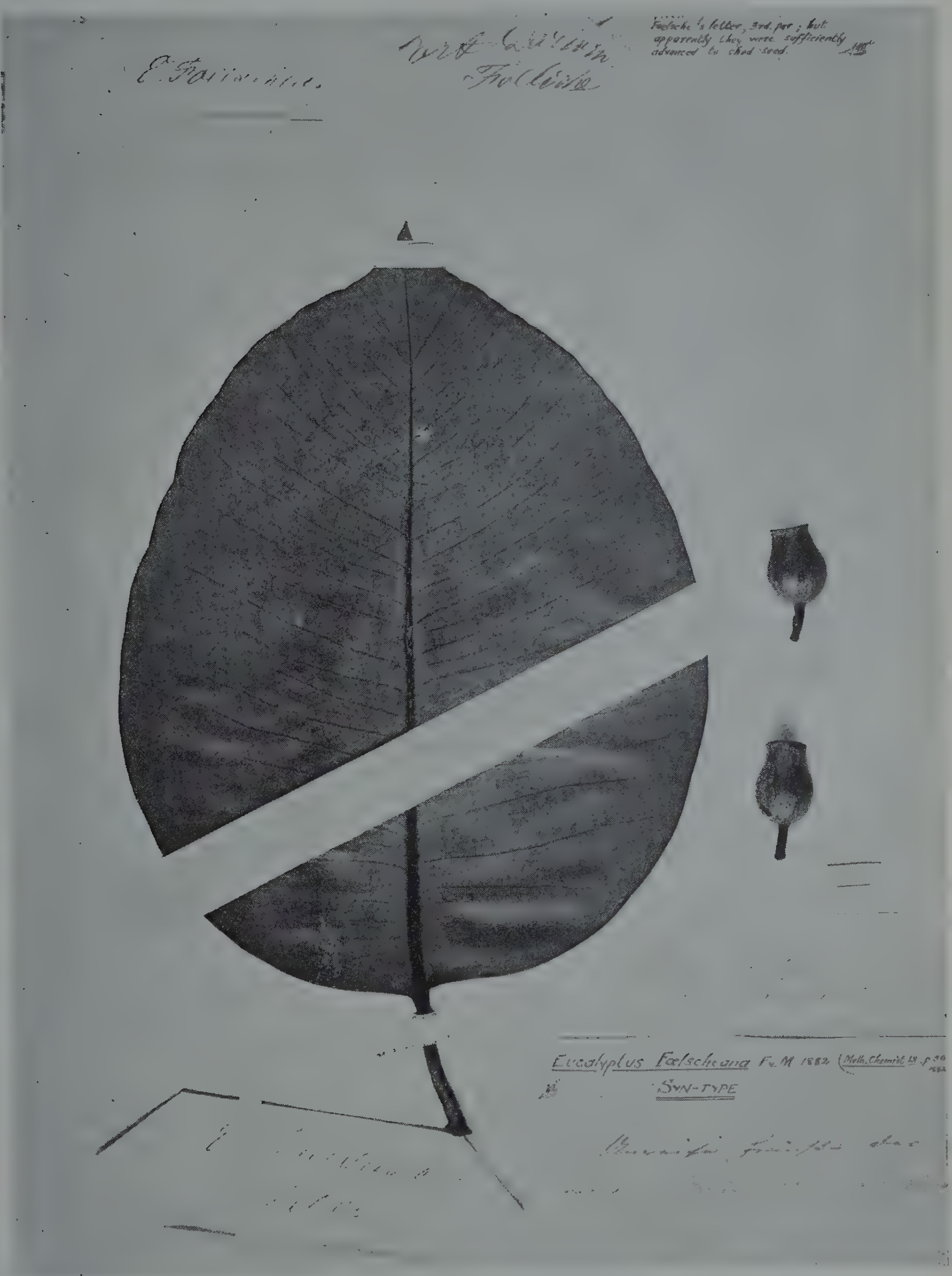
BARON FERD. VON MUELLER, PH. & M.D.

SYN-TYPE.

PHYTOLOGIC MUSEUM OF MELBOURNE.

Eucalyptus Foel-
scheana, F. v. M.
(North of Arnhem's Land
(vem. alta J. M'Kin

NORTHERN AUSTRALIAN SPECIES OF EUCALYPTUS


Foelsche's letter, 3rd. par.; but apparently they were sufficiently advanced to shed seed.
Port Darwin
Foelsche
Eucalyptus Foelscheana F. v. M. 1882 (Melb. Chemist ... p. 56 1882)
SYN-TYPE

NORTHERN AUSTRALIAN SPECIES OF EUCALYPTUS

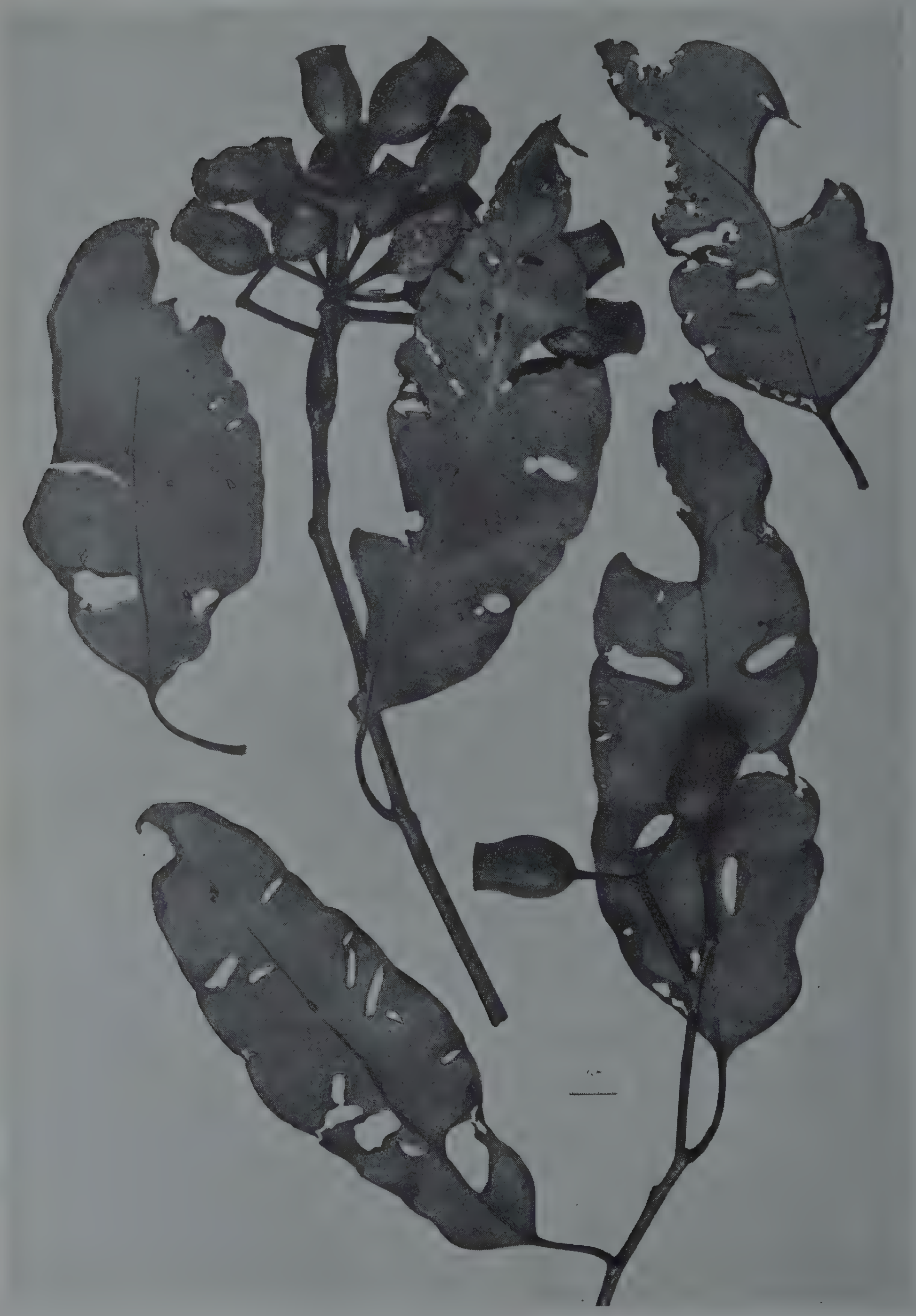
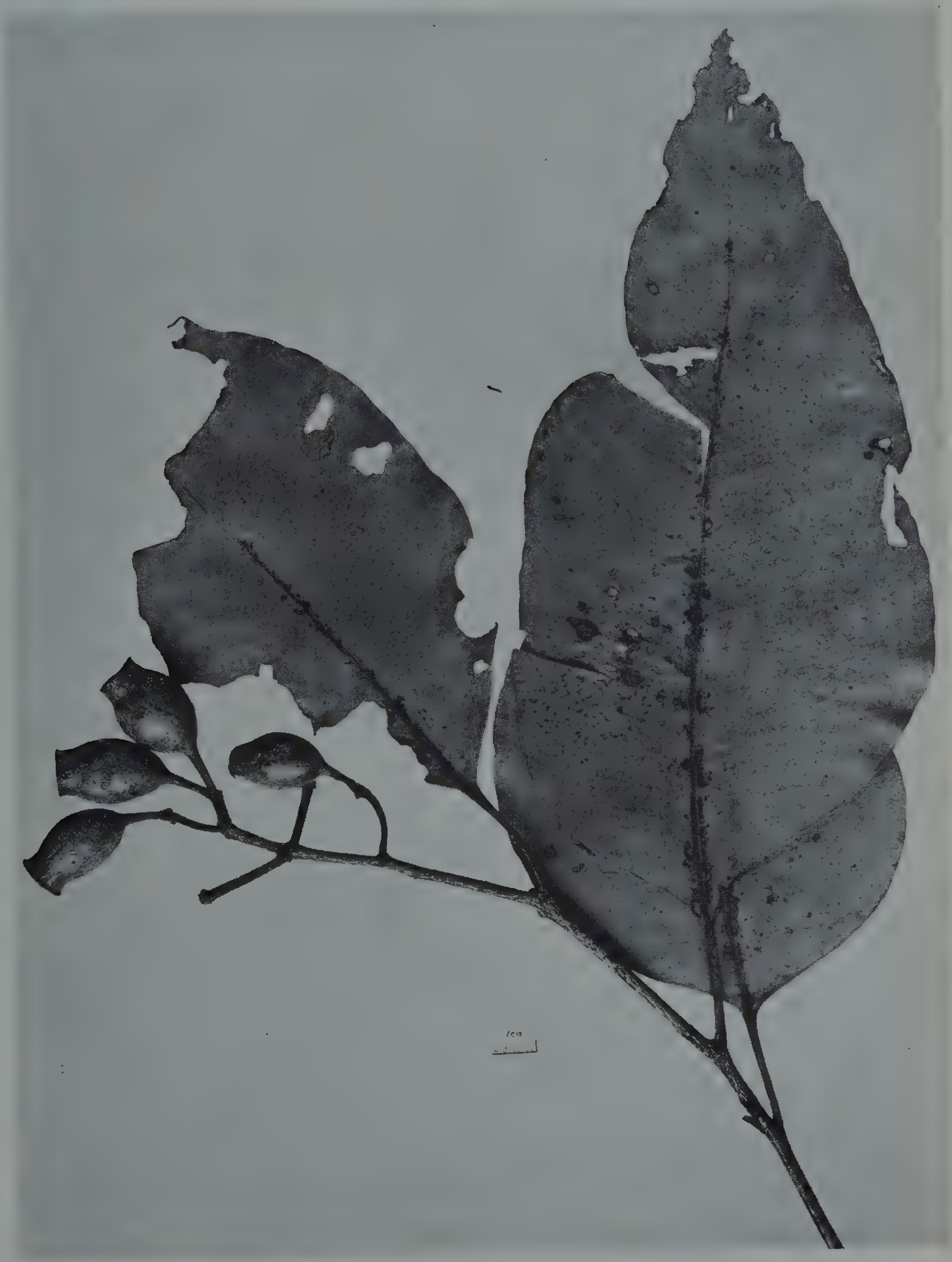


PLATE 21



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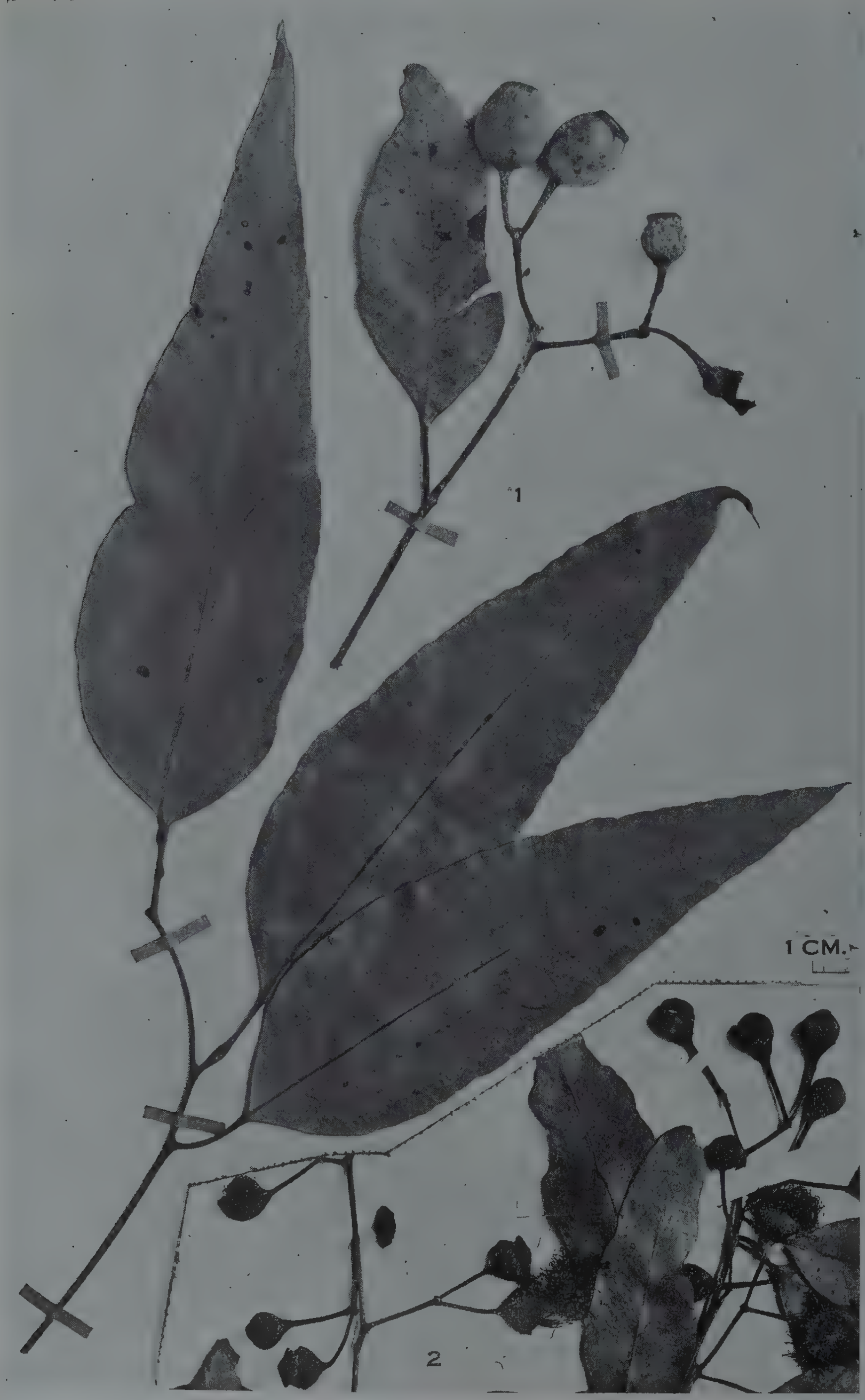

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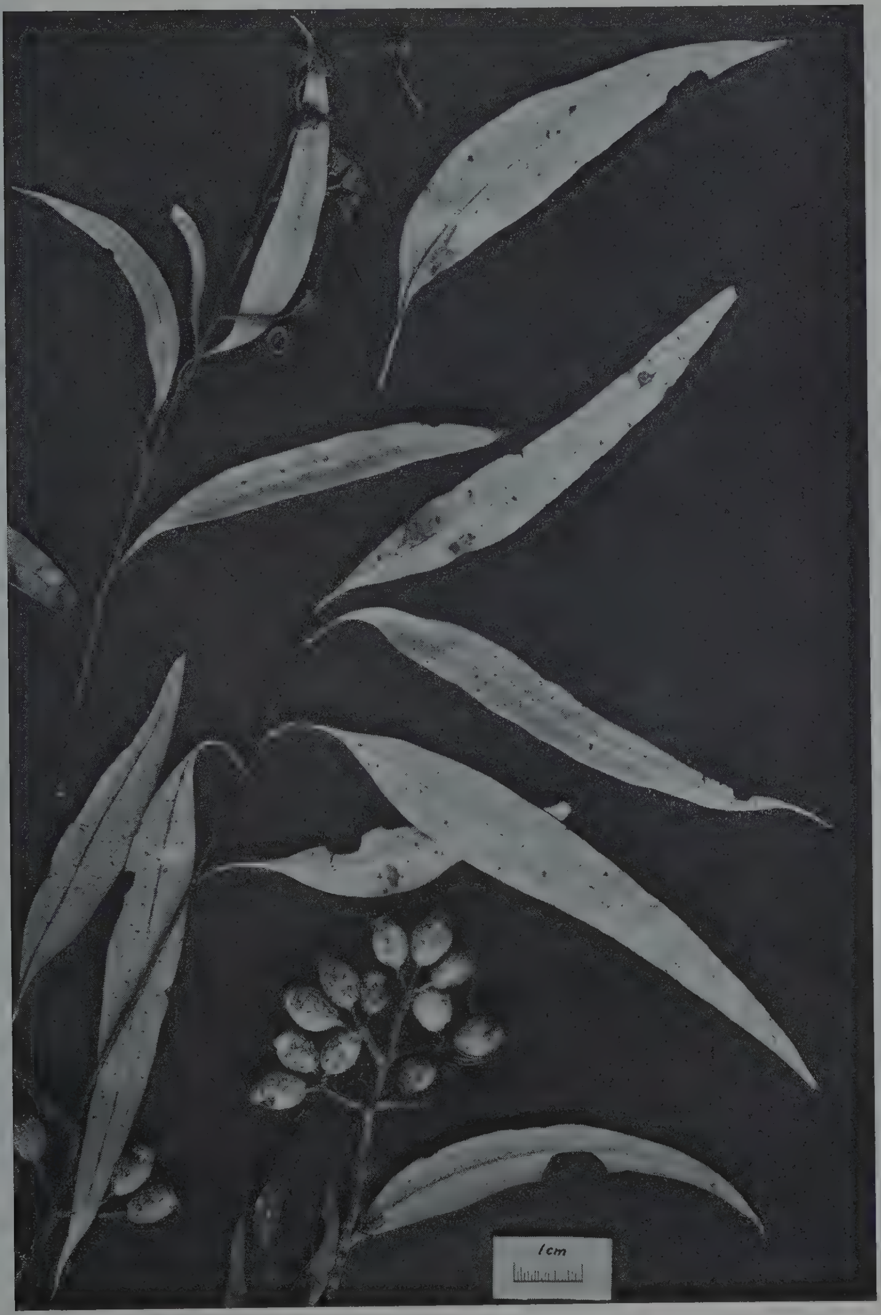

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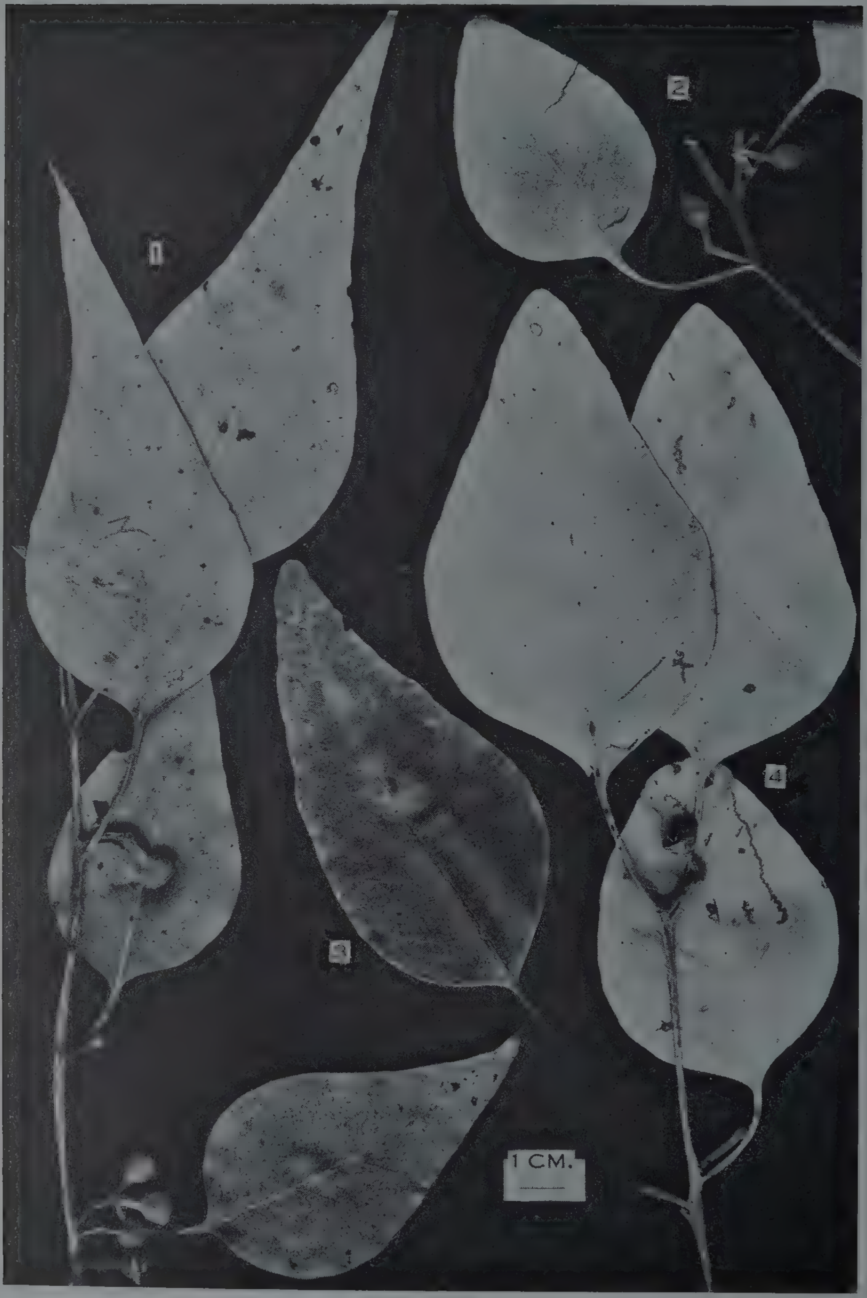

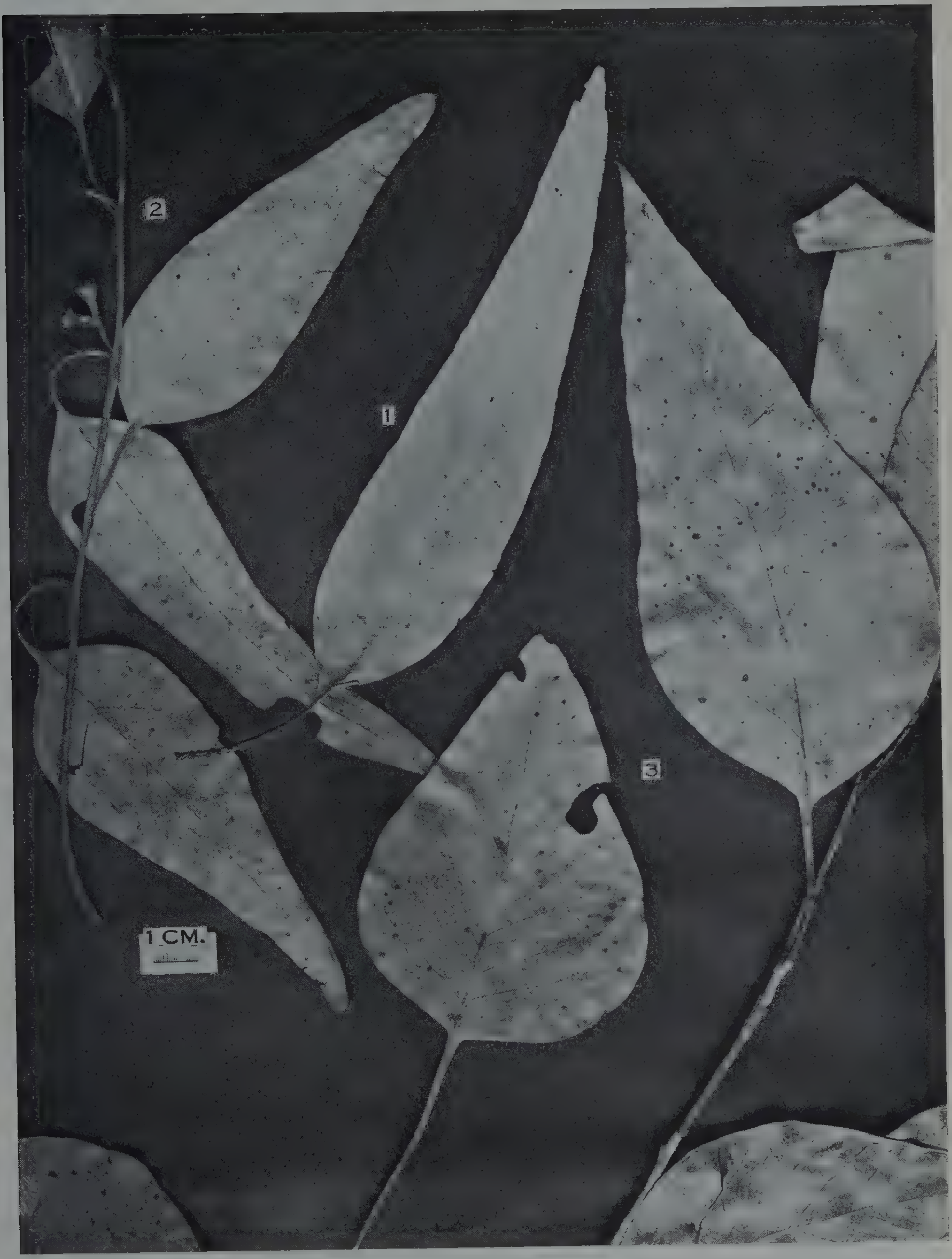
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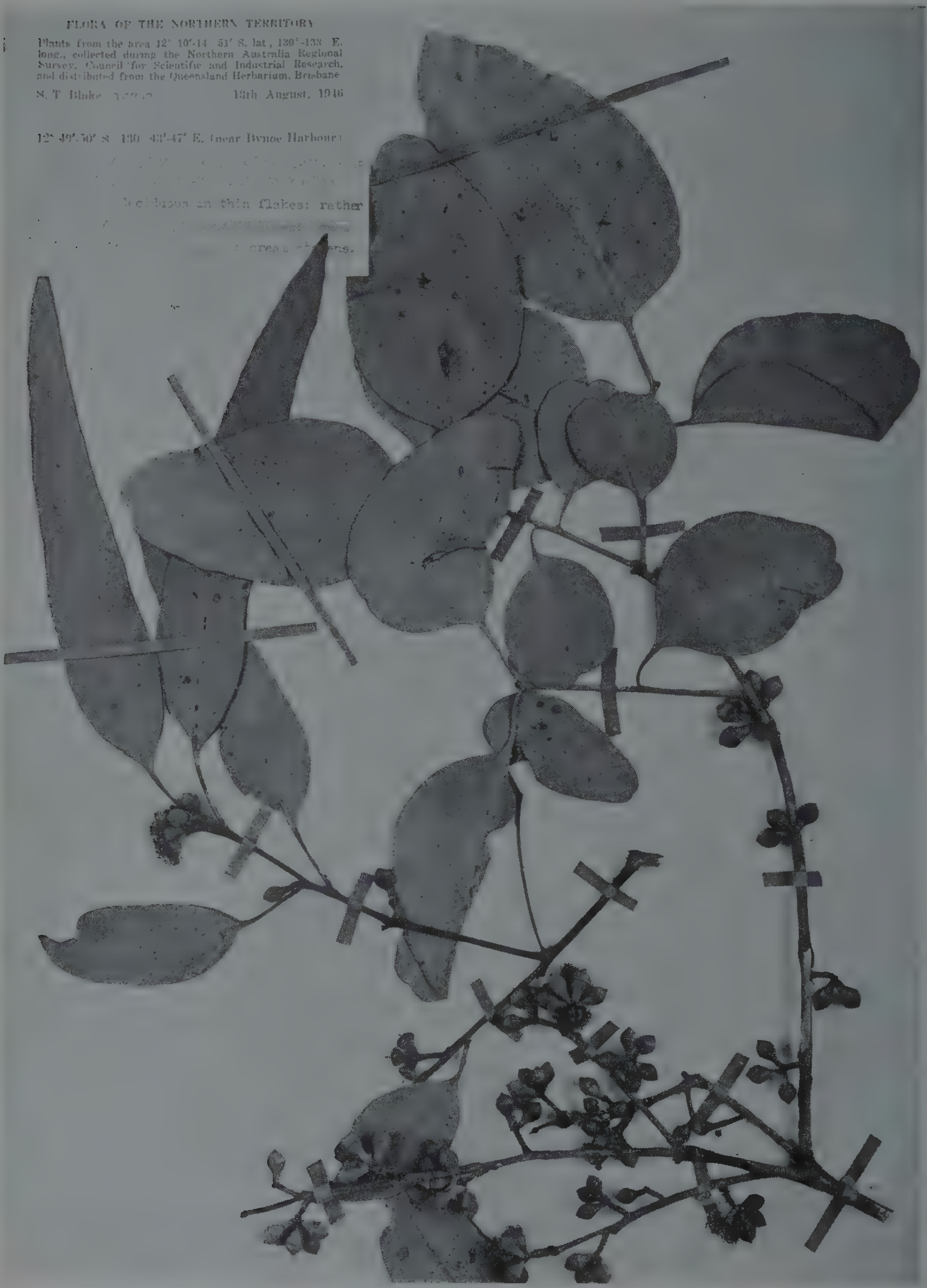
NORTHERN AUSTRALIAN SPECIES OF EUCALYPTUS



FLORA OF THE NORTHERN TERRITORY

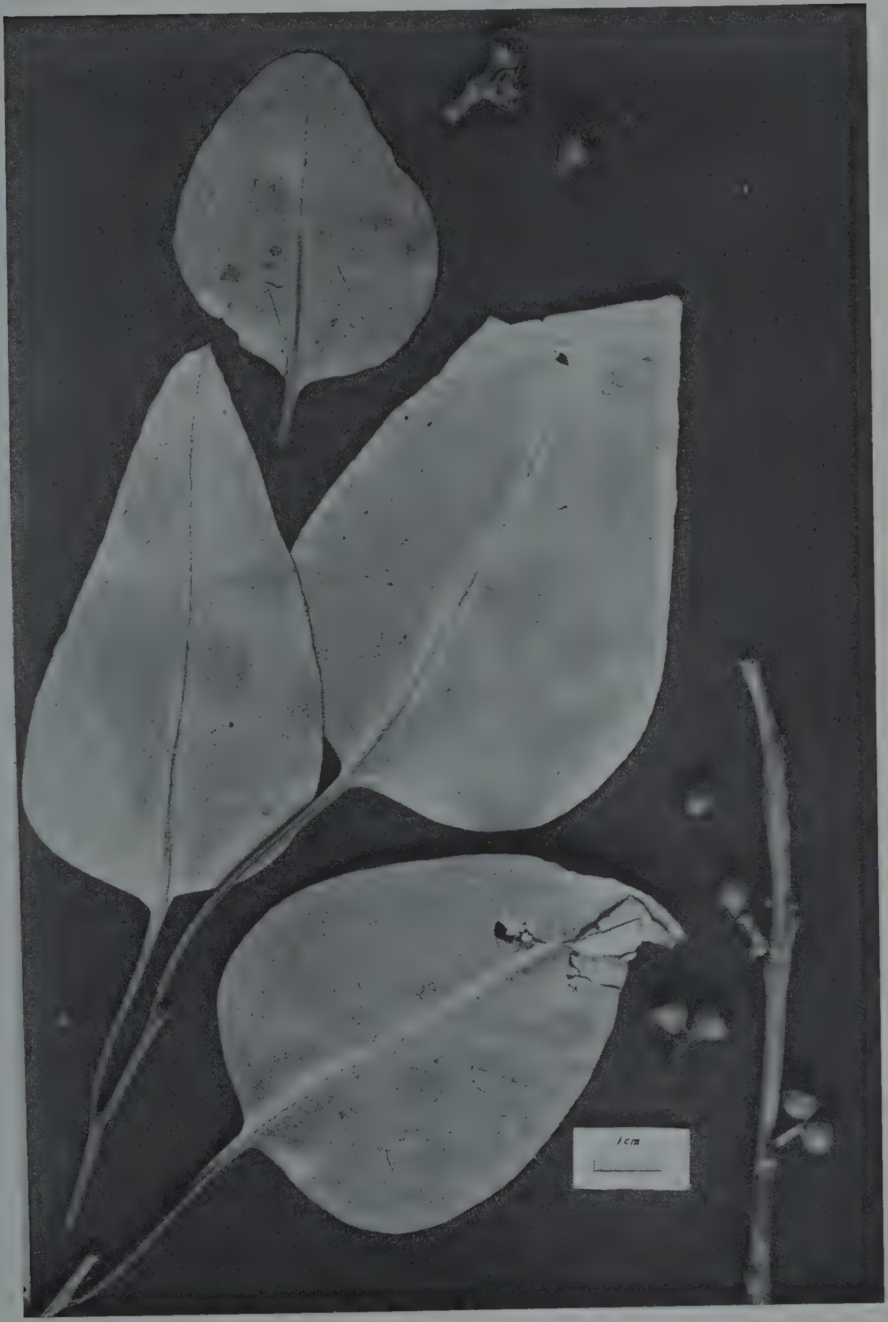
Plants from the area 12° 10′-14° 51′ S. lat., 130°-138° E. long., collected during the Northern Australia Regional Survey, Council for Scientific and Industrial Research, and distributed from the Queensland Herbarium, Brisbane

S. T. Blake [illegible] 13th August, 1946

12° 49′-50′ S. 130° 43′-47′ E. (near Bynoe Harbour)

[illegible] ciduous in thin flakes: rather [illegible]

[illegible] cream [illegible]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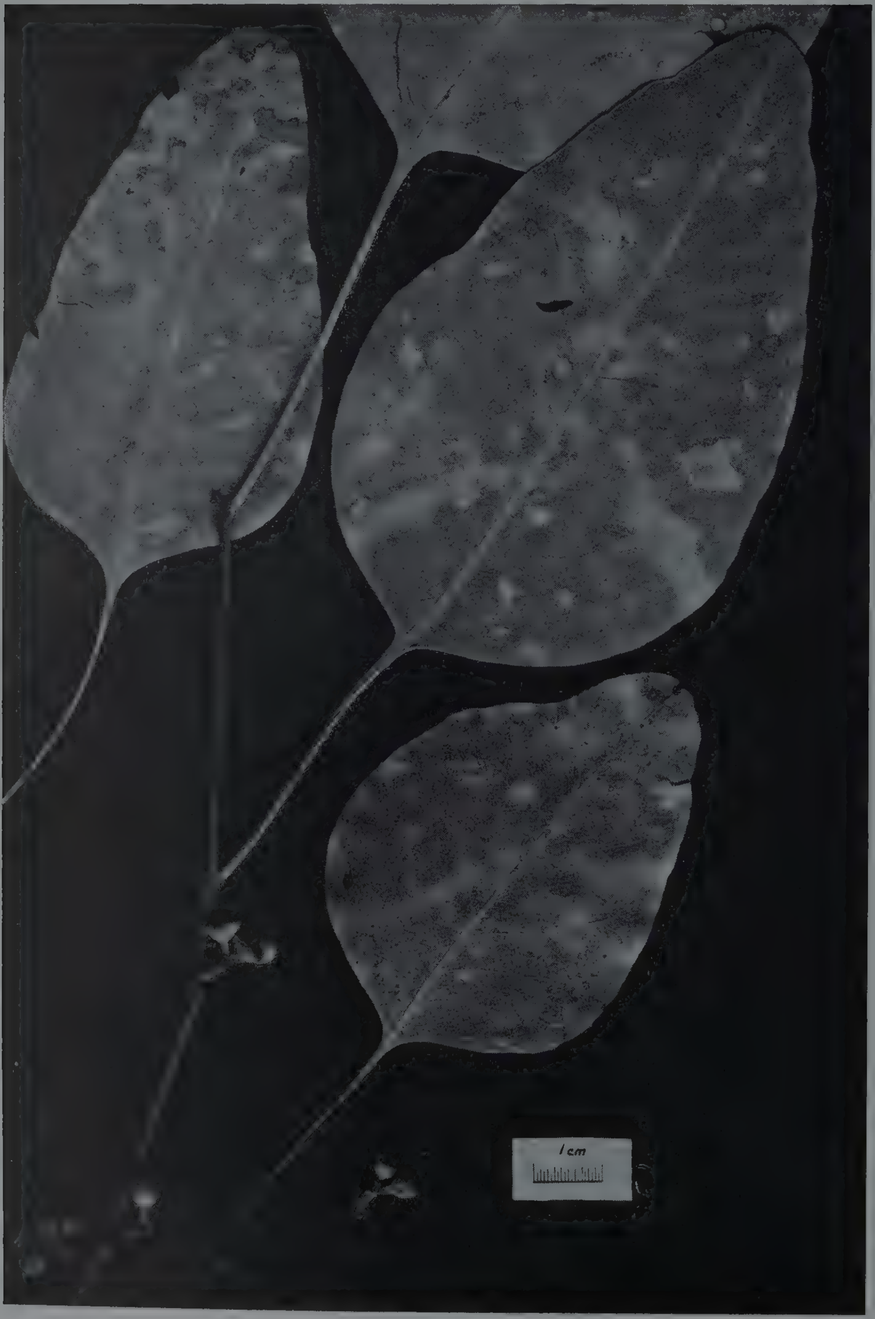
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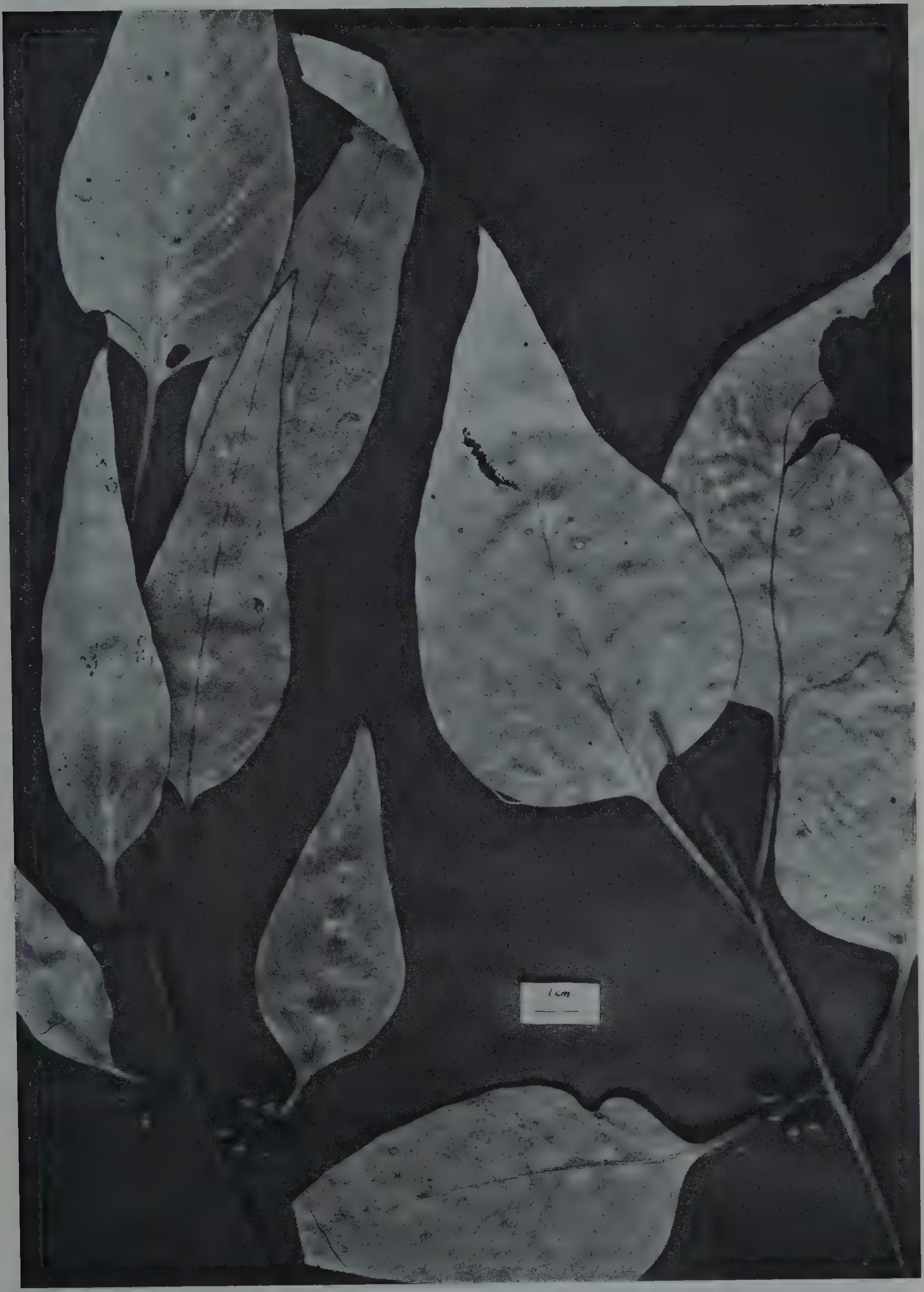
NORTHERN AUSTRALIAN SPECIES OF EUCALYPTUS



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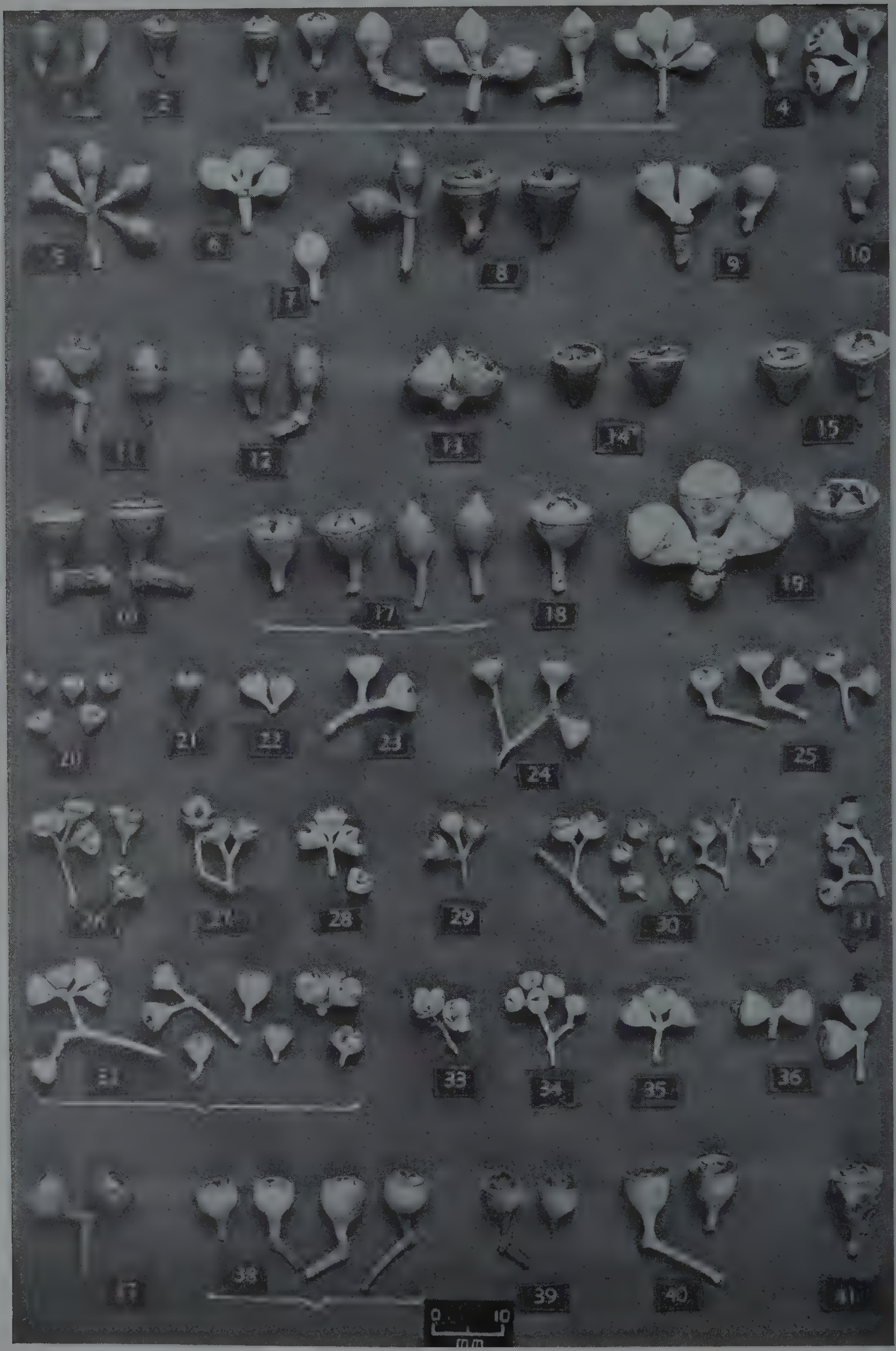
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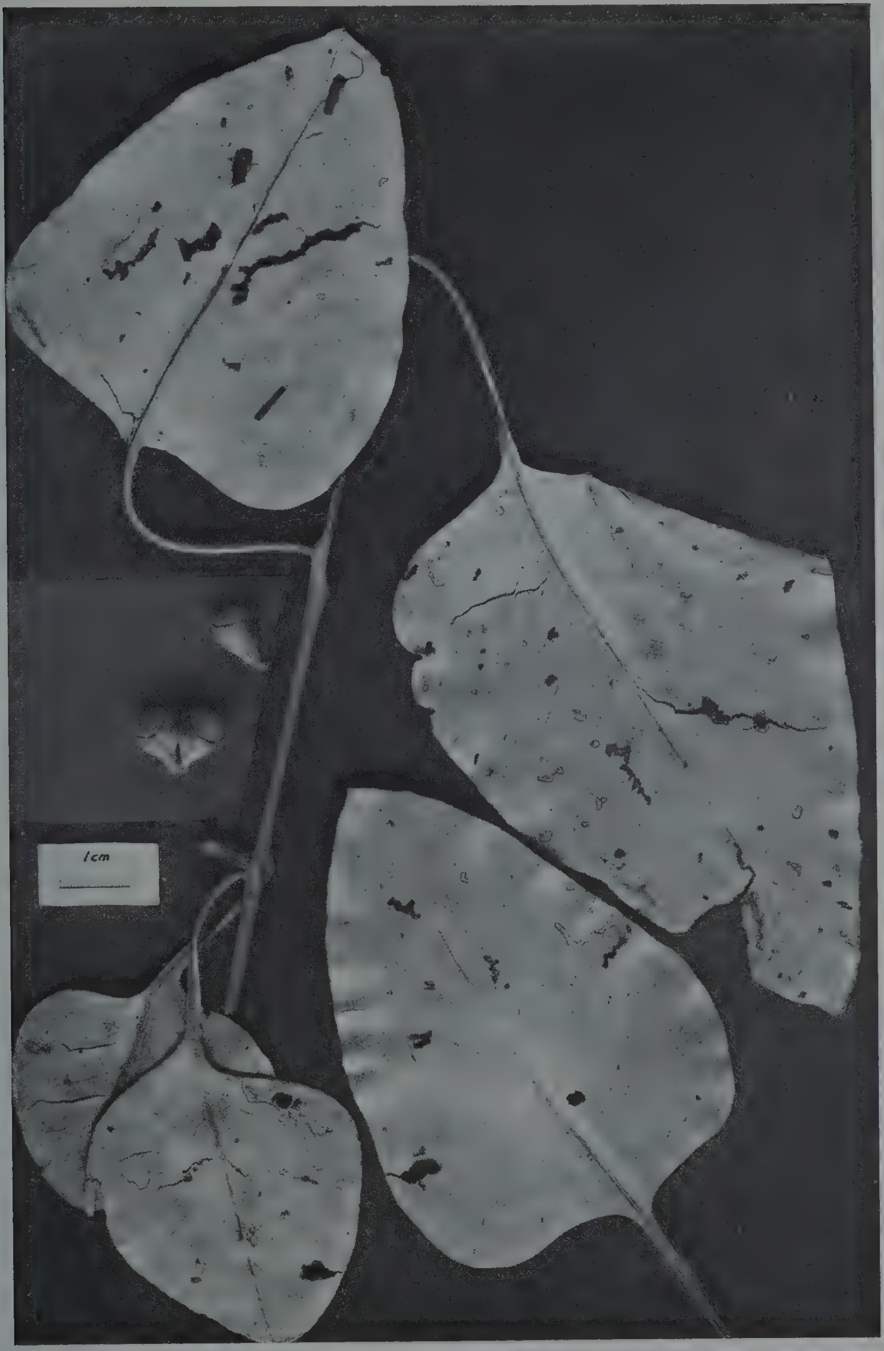
NORTHERN AUSTRALIAN SPECIES OF EUCALYPTUS



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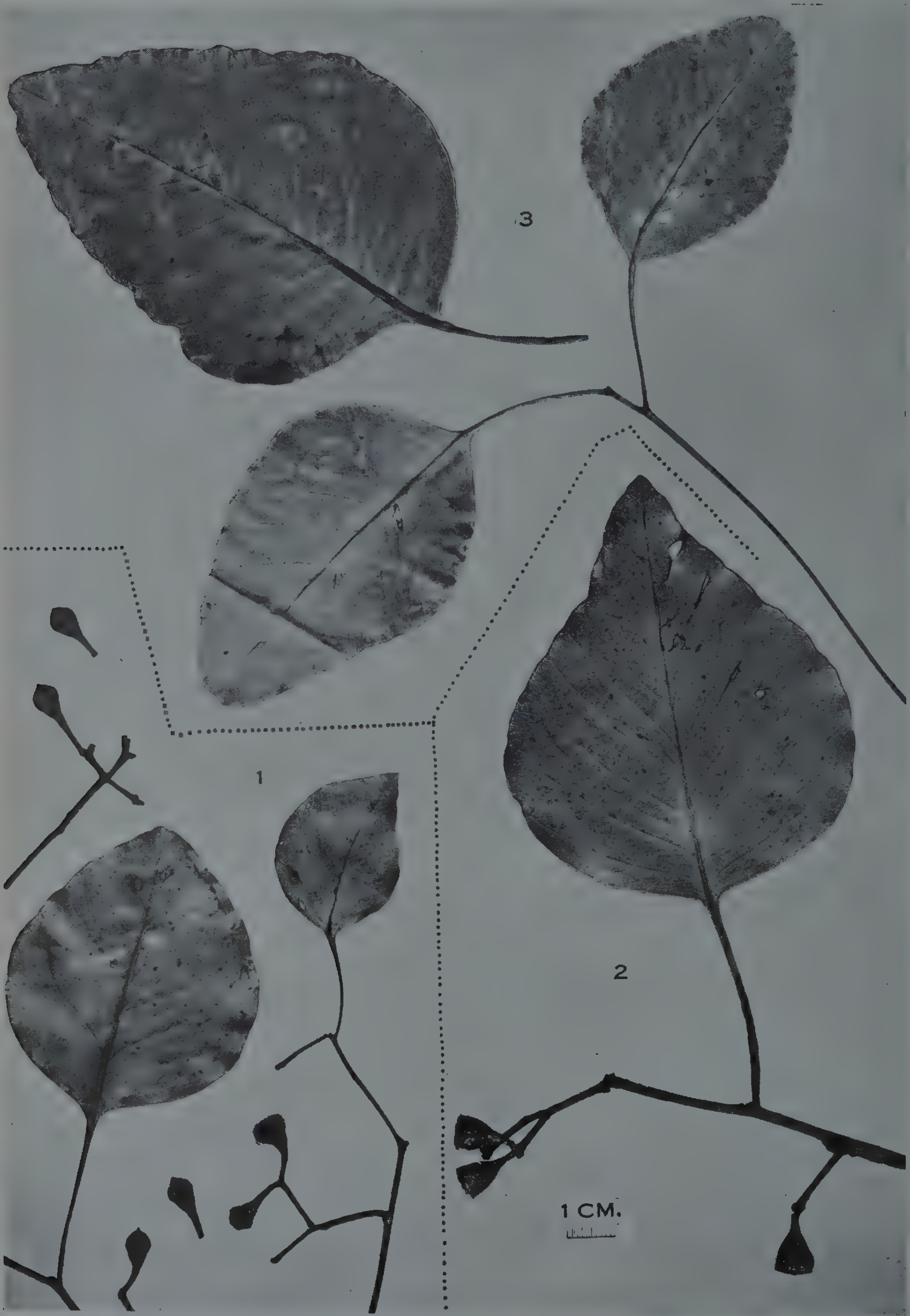

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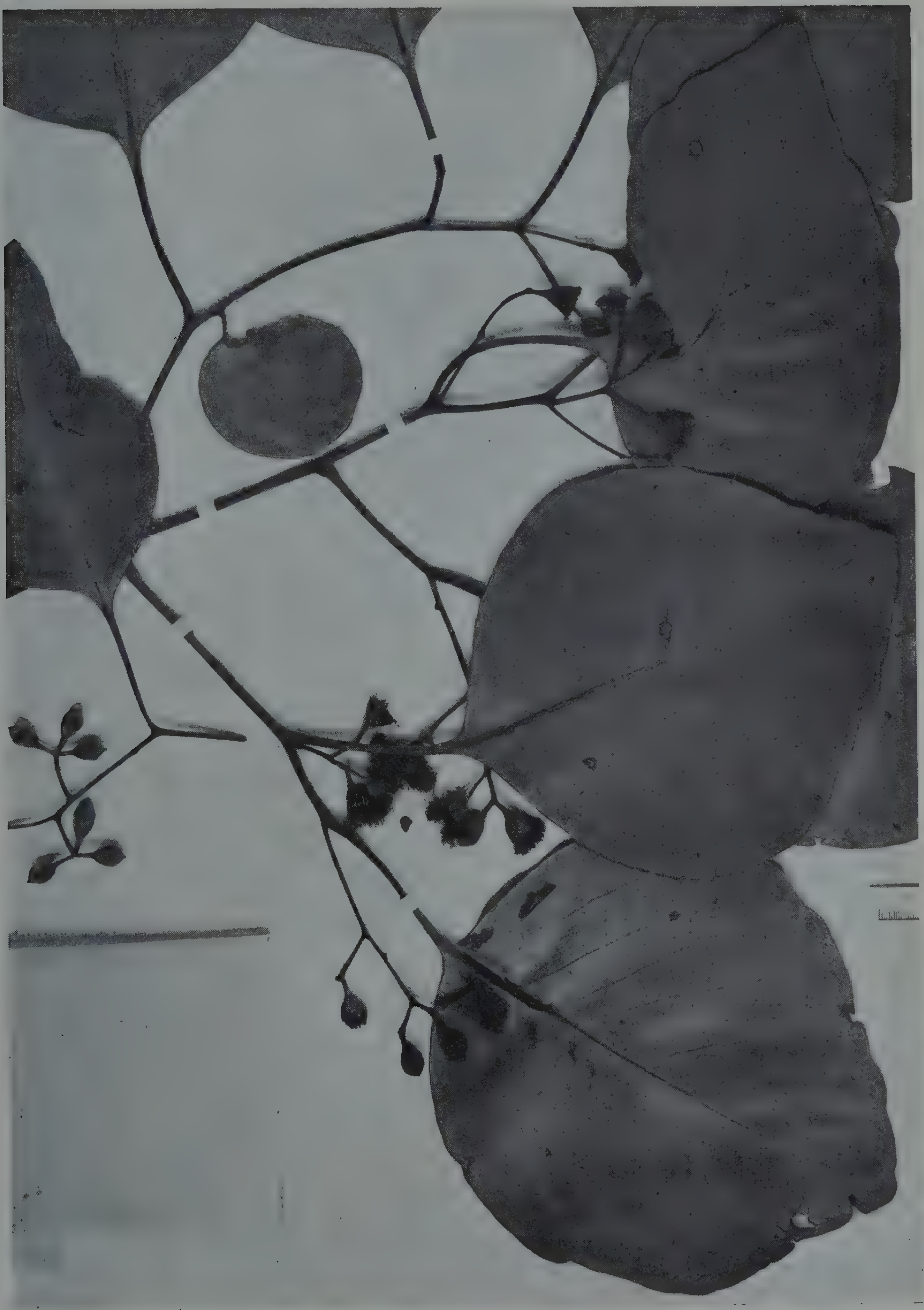

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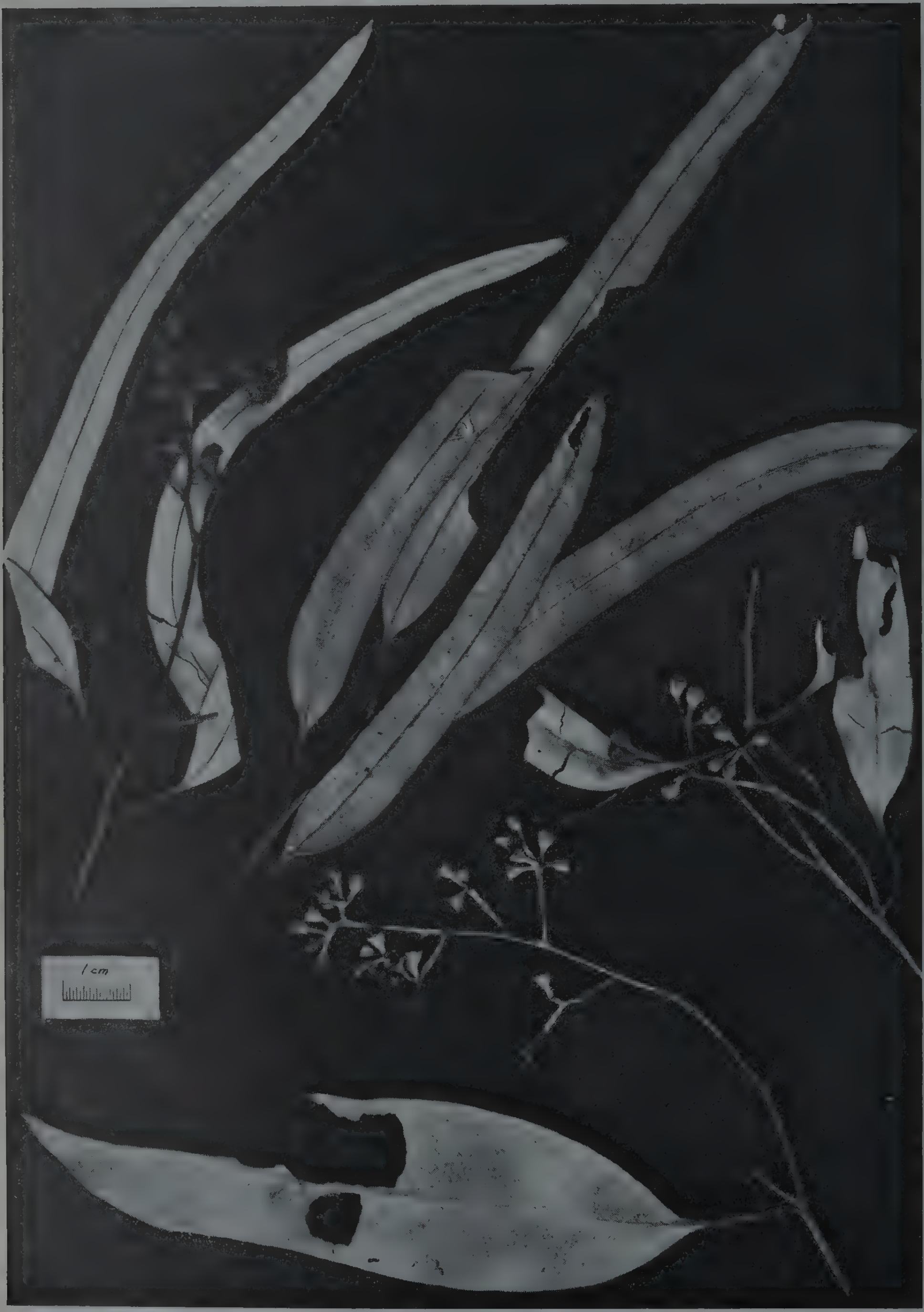

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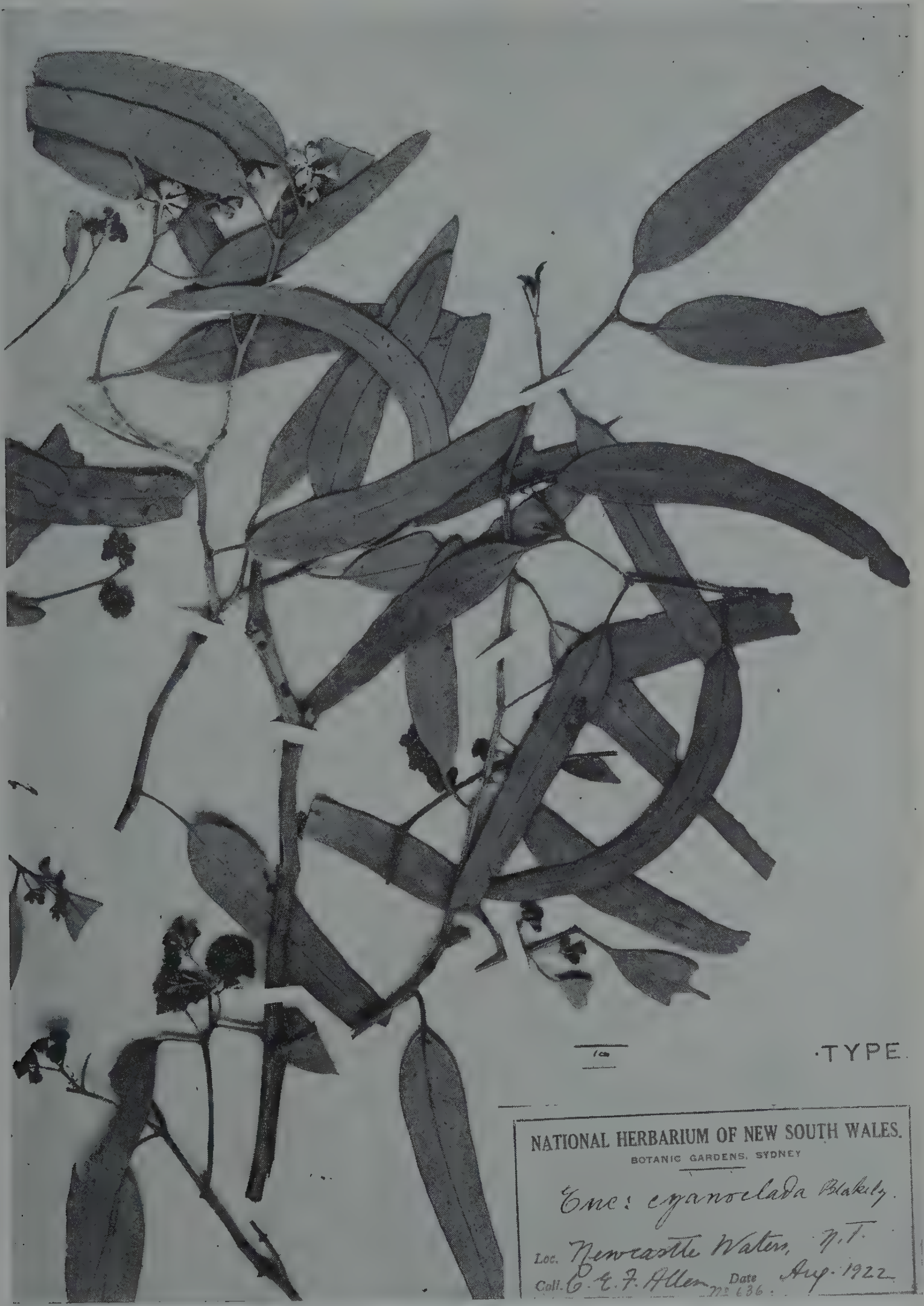
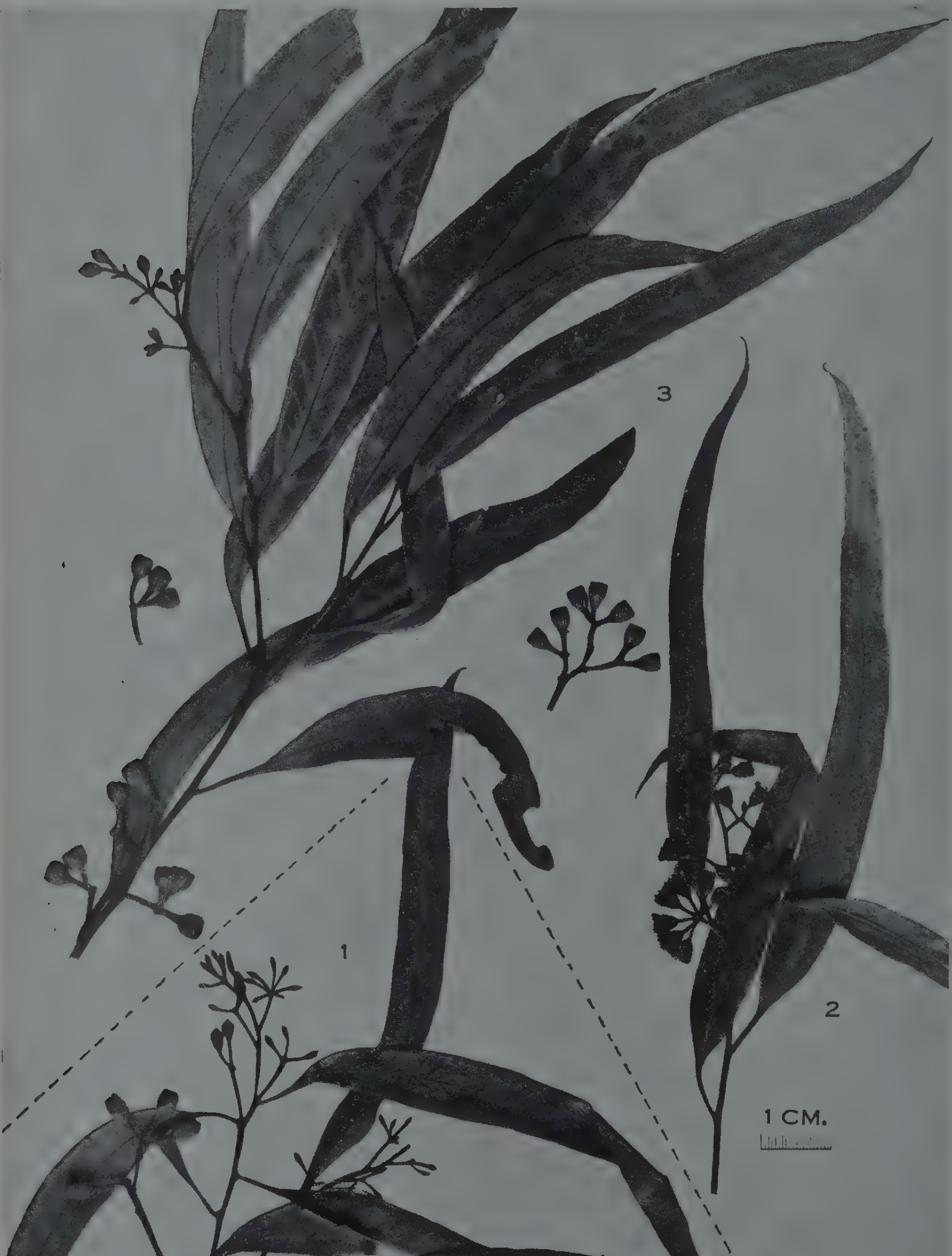


NATIONAL HERBARIUM OF NEW SOUTH WALES.
BOTANIC GARDENS, SYDNEY
Euc: cyanoclada Blakely.
Loc. Newcastle Waters, N.T.
Coll. C. E. F. Allen Date Aug. 1922
No 636.

NORTHERN AUSTRALIAN SPECIES OF EUCALYPTUS



THE ANATOMY OF THE TIMBERS OF THE SOUTH-WEST PACIFIC AREA

III. MYRTACEAE

By H. D. Ingle* and H. E. Dadswell*

[*Manuscript received January* 30, 1953]

Summary

The results reported form part of the series dealing with the timbers of the south-west Pacific area and cover 32 genera of the Myrtaceae.

The timbers of this family are perhaps more important, from an economic standpoint, than those of any other in the area under consideration (with the possible exception of the Dipterocarpaceae).

Based on the examination of all available species, the anatomical features of each genus have been summarized and the results set out in tabular form. From these a grouping of the genera of the family has been made, which reveals one or two inconsistencies with the botanical classification as proposed by Niedenzu. Particular mention has been made of the anatomical variation in *Eugenia* (sens. lat.).

The affinities of the described genera with those of the New World, and the anatomical differences between the Myrtaceae and the closely allied Lecythidaceae, are discussed. Anatomical features separating the Myrtaceae from four other families with some similar features have been pointed out.

I. General

The family Myrtaceae, which embraces some 90 genera and over 3,000 species of trees and shrubs, is spread through two main geographical areas, (i) the Australian region extending into the south-west Pacific area, and (ii) the American region, mainly central and tropical America. The more important, from the economic aspect, is the Australian region, where many of the tree species grow to a very large size (some to a height of 300 ft) and produce timbers with a world-wide reputation for strength and durability; e.g. species of the genus *Eucalyptus* L'Hérit.

In addition, *Eucalyptus* and other Australian genera are known for the essential oils derived from leaves and twigs. In the present study particular attention has been paid to the timbers of the family from the south-west Pacific area but some reference has been made to those from the American region for the purpose of comparing details of anatomical features. The objects of the investigation were (i) to bring together information on the anatomy of the various species of the family from the area under consideration, (ii) to develop methods for the identification of the woods of the various genera, and (iii) to consider generic relationships within the family as revealed by wood anatomy.

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* Division of Forest Products, C.S.I.R.O., South Melbourne.

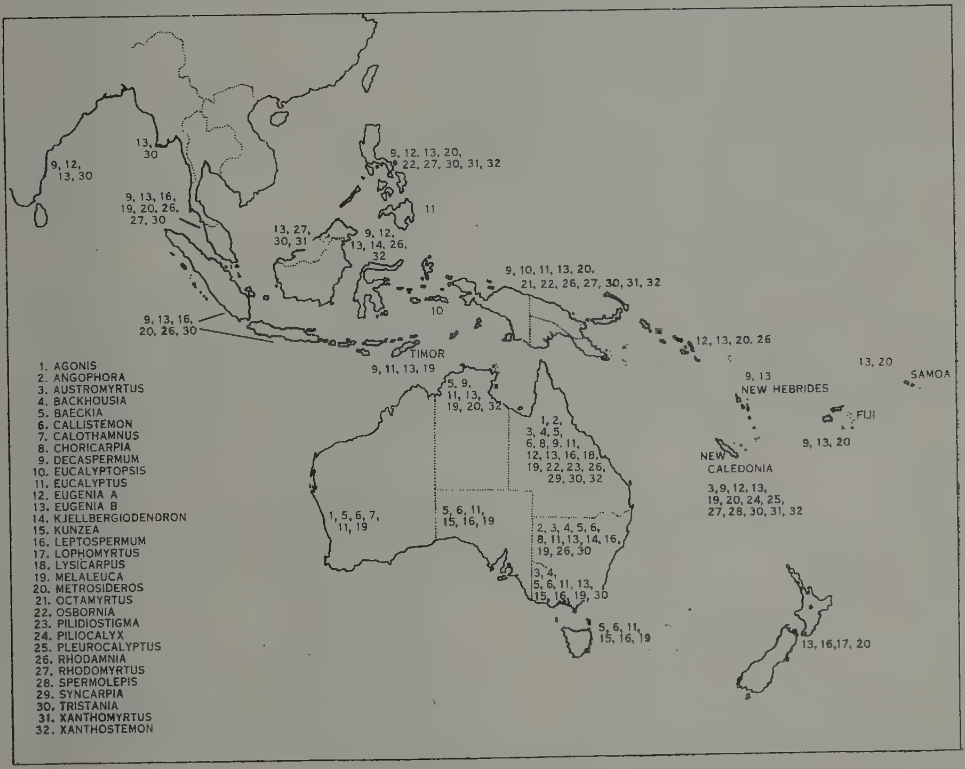
In a comparatively short paper, it is manifestly impossible to report in detail the anatomy of all the timber species examined. Therefore, summaries of anatomical features and the variations in these features have been recorded for each genus. Where applicable notes have been included relating to particular anatomical differences within a genus.

Originally the Myrtaceae included the Lecythidaceae, but it is now generally accepted that the two families are distinct. This conception is supported wood anatomically by the work of Diehl (1935); in the present investigation additional comparisons have been made. The botanical classification of the family developed by Niedenzu (1893) has been used as a basis for comparisons with groupings resulting from the examination of wood anatomy. This classification, with some slight modifications and additions resulting from the determinations of subsequent workers, is set out in Table 1, in which the genera represented in the present study have been indicated. In this table the genus *Kjellbergiodendron* Burret, first described in 1936 and referred to in a recent paper by Merrill (1952), has not been placed. It is botanically distinctive, having a more or less fleshy indehiscent, one-celled, and one-seeded fruit, characteristic of the Myrtoideae but with alternate leaves, not a feature of this subfamily. *Eucalyptopsis* White (White 1951) has, at the suggestion of the late Mr. C. T. White, been placed in the Metrosiderinae of the Leptospermoideae.

It is of interest to note that, of the two subfamilies into which Myrtaceae is divided, namely, Myrtoideae and Leptospermoideae, all the genera of the latter except *Tepualia,* a monotypic genus occurring in Chile, are confined to the south-west Pacific area. Many of the species of these genera are of Australian origin, for example, species of *Backhousia, Angophora, Syncarpia, Eucalyptus*; only five of the 600 + species and varieties of the last genus being in adjacent areas (Timor, New Guinea, Philippines). The tribe Chamaelaucieae, comprising 13 genera, is entirely Australian and mainly confined to the south-west portion of the continent. Species of these genera are all small to medium-sized shrubs and for this reason are not included in the present investigation. Twenty-five of the 39 genera of the Myrtoideae, which anatomically form a remarkably homogeneous group, are confined to tropical south and central America; the remainder are mainly from tropical Asia, Malaysia, and the Pacific, with a few species of two genera extending to Madagascar and the African continent. The distribution of the genera occurring in the south-west Pacific area covered by this work is shown in Figure 1.

The compilation of the information obtained from the anatomy of the various timber species has been complicated by the variation in the botanical concepts of certain genera. Since the time of Linnaeus many species from both the New and the Old World have been assigned to *Eugenia* L.; but modern concepts of this genus have been rather varied and it is considered by some botanical authorities that five, or perhaps six, distinct genera are represented. Niedenzu (1893) in his classification of the various genera within the Myrtaceae restricted *Eugenia* L. to the tropical American species and placed the great bulk of the Old World *Eugenia* species in *Syzygium* Gaertn. and *Jambosa* DC. Merrill and Perry accept one very large Old World genus, *Syzygium* Gaertn.

(including *Jambosa* DC. and *Caryophyllus* L.); in addition they have reinstated and revised *Cleistocalyx* Bl. and suggested that *Acmena* DC. is a valid genus (1937, 1938*a*). Both *Cleistocalyx* and *Acmena* are restricted to the Old World. Merrill has recently (1950*b*) followed Diels by accepting *Jossinia* Commers. to cover a small residue of Old World species which resembles certain of the American *Eugenia* species much more closely than they do the Old World *Syzygium* species. Other botanists (e.g. Henderson 1949) do not agree and retain all the Old World species in *Eugenia* L.; others while accepting *Syzygium* Gaertn. as distinct from *Eugenia* L., object to the separation of small genera such as *Cleistocalyx* and *Acmena* from *Syzygium* (Airy Shaw (1949) in Merrill 1950*b*).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1. AGONIS
2. ANGOPHORA
3. AUSTROMYRTUS
4. BACKHOUSIA
5. BAECKIA
6. CALLISTEMON
7. CALOTHAMNUS
8. CHORICARPIA
9. DECASPERMUM
10. EUCALYPTOPSIS
11. EUCALYPTUS
12. EUGENIA A
13. EUGENIA B
14. KJELLBERGIODENDRON
15. KUNZEA
16. LEPTOSPERMUM
17. LOPHOMYRTUS
18. LYSICARPUS
19. MELALEUCA
20. METROSIDEROS
21. OCTAMYRTUS
22. OSBORNIA
23. PILIDIOSTIGMA
24. PILIOCALYX
25. PLEUROCALYPTUS
26. RHODAMNIA
27. RHODOMYRTUS
28. SPERMOLEPIS
29. SYNCARPIA
30. TRISTANIA
31. XANTHOMYRTUS
32. XANTHOSTEMON

Fig. 1.—Distribution of genera examined in the south-west Pacific.

It is not the province of this paper to deal with these botanical concepts but it must be pointed out that the New World species of *Eugenia* differ markedly in their wood anatomy from the vast majority of the species that have been or might be referred to *Eugenia* L. from the south-west Pacific area (Dadswell and Ingle 1947). For these reasons, and as new combinations have not yet been made for many of the Australian species now placed in *Eugenia*, it has been difficult to deal with the anatomy of the genus as a whole. Therefore,

TABLE 1

CLASSIFICATION OF THE MYRTACEAE (AFTER NIEDENZU 1893)

		Genera Subsequently Recognized
I. Myrtoideae—Fruit a berry, rarely a drupe Myrteae		
A. Stamens erect in the bud, but after flowering spread out. Endosperm present? Embryo upright, radicle about as long as the leaf-like cotyledons .. .. .. Orthostemoninae	*Orthostemon** Berg (= *Feijoa* Berg)	
B. Stamens in the bud almost their ultimate length and nearly always bent inwards. Endosperm lacking. Embryo usually bent, or the cotyledons folded or fleshy:		
a. Embryo horse-shoe-shaped or spirally rolled; radicle usually much bigger than the small cotyledons .. .. .. Myrtinae		
1. Testa of seed horny:		
i. Ovary unilocular; both placentas parietal	*Rhodamnia**† Jack	
ii. Ovary multilocular; rarely unilocular, through the abortion of 1 placenta, leaving the ovary unilocular	*Ugni* Turcz. *Calycolpus** Berg. *Myrteola* Berg. *Myrtus** L. *Psidium* L. *Psidiopsis* Berg. *Myrrhinium* Schott. *Decaspermum**† Forst. *Rhodomyrtus**† DC. *Fenzlia*† Endl.	*Krokia** Urb. *Anamomis** Griseb. *Lophomyrtus** †Burret *Austromyrtus**† Burret *Xanthomyrtus**† Diels
2. Testa of seed membranous:	*Blepharocalyx** Berg. *Pimenta** Lindl. *Mitranthes* Berg. (= *Calyptranthes** B. & H.) *Acrandra* Berg. *Campomanesia* Ruiz. & Pav. *Britoa* Berg. *Paivaea* Berg.	*Octamyrtus**† Diels *Pilidiostigma**† Burret
b. Radicle and cotyledons about equal in length; the latter leaf-like and crumpled up together .. .. .. Myrciinae		
1. Number of seeds in each locule indefinite	*Myrceugenia* Berg.	

TABLE 1 (*Continued*)

		Genera Subsequently Recognized
2. Two seeds, side by side, in each locule	*Myrcia** DC. *Marlieria* Camb. *Calyptranthes** Swarz. *Gomidesia** Berg.	
c. Radicle generally very short and bent back against the large, thick, fleshy cotyledons .. .. .. Eugeniinae		
1. Ovary central in calyx tube, which has a distinct pedicel	*Eugenia** L. *Calycorectes* Berg. *Myrciaria** Berg. *Aulacocarpus* Berg.	*Jossinia**† Commers.
2. Calyx tube usually considerably extended beyond the ovary, constricted into a single unit with the pedicel; ovary in the upper part	*Jambosa**† DC. *Syzygium**† Gaertn. *Acicalyptus**† A. Gray *Piliocalyx**† Brongn. & Gris.	*Acmena**† DC. *Cleistocalyx**† Bl. (incl. *Acicalyptus* A. Gray)
II. Leptostermoidae—Fruit dry:		
A. Ovary, at least in rudimentary stage, multilocular, usually dehiscent .. Leptospermeae		
a. Embryo straight, or slightly bent, cotyledon nearly as long as, or longer than the radicle:		
1. Fruit a schizocarp or achene. Anthers versatile .. .. .. Backhousiinae		
i. Eight sepals, no petals; ovary incompletely subdivided; fruits not separated	*Osbornia**† F. Muell.	
ii. Four sepals, 4 petals; ovary incompletely subdivided; fruits separated, falling singly	*Backhousia**† Hook. & Harv.	
2. Fruit a loculicidal capsule. Anthers versatile:		
i. Inflorescence usually axillary, umbel, seldom solitary; petals attached by a narrow base .. Metrosiderinae		
a. Stamen free in a single ring more or less evenly distributed	*Metrosideros**† Banks *Spermolepis**† Brongn. & Gris. *Lysicarpus**† F. Muell. *Cloezia**† Brongn. & Gris. *Tepualia** Griseb. *Syncarpia**† Ten. *Xanthostemon**† F. Muell. *Pleurocalyptus**† Brongn. & Gris.	*Choricarpia**† Domin. *Eucalyptopsis**† White

TABLE 1 (*Continued*)

CLASSIFICATION OF THE MYRTACEAE (AFTER NIEDENZU 1893)

		Genera Subsequently Recognized
β. Stamens in groups opposite the petals, more or less coalescent ..	*Tristania**† R. Br.	
ii. Inflorescence usually axillary, umbel, petals attached by a broad base .. .. .. Eucalyptinae		
α. Sepals distinguishable as pronounced teeth	*Angophora**† Cav.	
β. Sepal teeth almost indistinguishable or lacking; petals coalescent, forming a distinct cup	*Eucalyptus**† L'Hérit	
iii. Flowers solitary in the axils of leaves or bracts; petals attached by a narrow base .. .. Leptosperminae		
α. Stamens shorter than the petals, free from one another	*Leptospermum**† Forst. *Agonis**† DC.	
β. Stamens longer than the petals	*Kunzea**† Reichb. *Callistemon**† R. Br. *Melaleuca**† Linn. *Lamarchea*† Gaud. *Conothamnus*† Lindl.	
3. Fruit a loculicidal capsule, anthers basifixed .. .. Calothamninae	*Calothamnus*† Lab. *Beaufortia*† R. Br.	
b. Cotyledons folded back towards the radicle, small; radicle thick .. .. Baeckeinae	*Baeckia**† Linn.	
B. Ovary unilocular from the beginning; fruit nut-like, usually one-seeded .. Chamaelaucieae Floral axis may or may not be extended beyond the ovary. Ovary unilocular, mostly 1-4 seeds, seldom up to 10; fruit dry, achene mostly unilocular	*Thryptomene*† Endl. *Verticordia*† DC.	

* Genera examined at least in part in this work.

† Genera occurring in the south-west Pacific.

descriptions have been set out under two headings, namely, *Eugenia A,* covering the few species from the Pacific region which agree anatomically with the New World species (it is possible that botanically some or all of these species fall in *Jossinia* Commers.); and *Eugenia B,* covering *Syzygium* and those species similar in wood anatomy but for which new combinations have not yet been made. Dadswell and Ingle (1947) did not observe any clear-cut anatomical distinction between *Syzygium, Acmena,* and *Cleistocalyx,* and in this paper all three genera, although treated separately, have been grouped together for convenience of comparison under *Eugenia B.*

Myrtus L. has been restricted by Burret (1941*b*) to cover species from Central and South America and two species from the Mediterranean region. He has transferred species from the south-west Pacific area, previously included in it, to other genera including *Lophomyrtus, Austromyrtus, Uromyrtus, Neomyrtus, Rhodomyrtus, Pilidiostigma,* and *Myrtastrum.* Several of the Australian species have been placed in *Austromyrtus* together with a number of New Caledonian species previously in *Myrtus* L. and *Eugenia* L. The New Zealand species have been transferred to *Lophomyrtus* (three species) and *Neomyrtus* (one species). *Pilidiostigma* covers one species formerly in *Myrtus* and a few new Australian species; the species referred to *Uromyrtus* and *Myrtastrum* occur in New Caledonia. In the present investigation species of *Austromyrtus, Lophomyrtus, Pilidiostigma,* and *Rhodomyrtus* were available for examination.

The genus *Eucalyptus* has been considered under two main groups — *Eucalyptus A,* covering the great majority of this genus, and *Eucalyptus B,* covering the species generally known as "bloodwoods." Considerable attention has been paid (Dadswell and Burnell 1932; Dadswell, Burnell, and Eckersley 1934) to the anatomy of the various species of this genus and methods of identification of the various timbers are being extended and revised.

Details of the timbers of the family occurring in certain regions have been given by various workers, including Pearson and Brown (1932), Janssonius (1908), Reyes (1938), and Record and Hess (1943). Metcalfe and Chalk (1950) have summarized the anatomical features of the family, covering 19 of the genera examined in these investigations.

For this investigation material was obtained from the standard collection of the Division of Forest Products, C.S.I.R.O.; which includes various authenticated specimens received through the courtesy of forestry authorities in Malaya, North Borneo, Indonesia, the Philippines, New Guinea, the British Solomon Islands, New Caledonia, and New Zealand.

II. The Anatomical Characteristics of the Genera Examined

All available wood specimens of each species within a genus were examined macroscopically and microscopically and the results summarized. From the species summaries the generic descriptions were prepared. Details of the observed anatomical features for each genus have been set out in Table 2. Both in the generic descriptions and in the table averages of maximum vessel diameter, vessel member length, fibre length, and diameter of the borders of vessel pits have been recorded. Because of variations within a tree, within a species, and between species, these measurements are not necessarily helpful in separating many of the genera, nevertheless certain interesting trends have been observed.

Macerated material from each available specimen was used for the measurements of vessel member length; 10 vessel members were selected at random in each and their lengths measured from tip to tip. The average for each species was thus obtained and the range of vessel member lengths for the genus recorded. The size-classes used in the descriptions were those suggested by Chattaway (1932). The maximum tangential diameter of vessels was obtained for every specimen by making 20 measurements and averaging the 10 largest. The recorded range for each genus was based on the averages for the various species within the genus.

As fibre length varies considerably according to position within the tree, and in some instances even within a growth ring, measurements were made of 50 fibres taken at random from macerated material taken over several growth rings of mature wood, i.e. wood several inches from the centre of the tree, of each specimen. The recorded figures give an indication of the range of average fibre lengths within each genus.

The diameters of the vessel pits were measured in each specimen and a record made of the smallest and largest pits within each species. In the generic descriptions and Table 2 the range given covers the smallest to the largest pits in all the species examined for each particular genus.

The presence or absence of tracheids was determined from the examination of macerated material.

(*a*) *Agonis*

(i) *General.*—A genus of some 13 species of shrubs and small trees confined to Australia. Specimens from two species were available for examination. The heartwood is brown, pinkish brown to red-brown, fine-textured, moderately heavy to heavy.

(ii) *Structure.*—*Growth rings* visible macroscopically, in *A. flexuosa* owing to differences in fibre wall thickness and in *A. juniperina* to a concentration of pores in the early part of the growth ring. *Vessels* small and indistinct to the naked eye; maximum tangential diameters 116-130 μ; mean member length 390-520 μ; solitary, occasional radial or tangential multiples in *A. flexuosa*; solitary (60 per cent.) and in clusters, oblique or tangential multiples, often zonate in oblique or tangential arrangement in *A. juniperina*; generally oval in shape with radial axis elongated; moderately numerous to numerous, 6-12/sq. mm; vessel pitting bordered, alternate, vestured, diameter 5-8 μ; perforation plates simple. *Vasicentric tracheids* common. *Rays* 1-4-seriate, uniseriate rays low, generally less than 8 cells, and moderately abundant, multiseriate rays weakly heterogeneous, the marginal cells tending to be of greater vertical dimension than the procumbent central cells; vessel-ray pitting half-bordered and similar to the inter-vessel type; deposits of extraneous material present; no silica or crystals observed. *Parenchyma* moderately abundant, paratracheal to sometimes confluent (Plate 6, Fig. 2) and also diffuse in *A. flexuosa,* sparse diffuse in *A. juniperina*; occasional enlarged crystal-bearing cells observed in *A. flexuosa. Fibres* thick-walled to moderately thin-walled (*A. juniperina*), non-septate with numerous small but distinctly bordered pits; mean length 0.81-1.05 mm.

(iii) *Material.*—*Agonis flexuosa* Lindl., four samples Western Australia; *A. juniperina* Schauer, two samples Western Australia.

(*b*) *Angophora*

(i) *General.*—A small genus of medium-sized to occasionally large trees confined to Australia, specimens from seven species were available for examina-

Table 2

SUMMARY OF ANATOMICAL CHARACTERISTICS OF 32 GENERA OF THE MYRTACEAE OCCURRING IN THE SOUTH-WEST PACIFIC AREA

Genus	No. of Species Examined	Vessels				Rays								Parenchyma								Fibre Pits Conspicuously Bordered	Vasicentric Tracheids	Mean Fibre Length (mm)
										Vessel-ray Pitting				Apotracheal		Paratracheal			Abaxial	Crystals				
		Percentage Solitary	Max. Tangential Diameter (μ)	Mean Member Length (μ)	Diameter of Pit Borders (μ)	Predominant Widths† (no. of cells)	Marginal Cells Upright 3+	Weakly Heterogeneous	Silica	Small, Similar to Vessel Type	Small, Simple Round to Elongated	Simple Elongated to Scalariform	Large, Simple (Eucalypt)	Diffuse	Tending to Short Lines or Bands	Paratracheal to Vasicentric	Confluent	Wide or Narrow Bands		Strands	Enlarged; Solitary or in Strands			
Agonis	2	65-90	116-130	390-520	5-8	1-4	−	+	−	+	−	−	−	+	−	+	∓	−	−	−	±(1)	+	+	0·81-1·05
Angophora	7	35-60	190-210	370-580	8-12	1-2	−	+	−	−	−	−	+	+	−	+	+	±	−	+	−	+	+	0·70-1·20
Austromyrtus	3	95	48-115	620-880	4-6	1, (2), 3-4	+	−	−	+	−	−	−	+	+	±	−	−	±	−	−	+	+	1·15-1·55
Backhousia	4	100	85-175	530-780	4-8	1-2 (3)	−	+	−	+	−	−	−	+	±	−	−	−	±	±	−	+	−	0·85-1·55
Baeckia	1	100	72	550	4-6	1-2	−	+	−	+	−	−	−	+	−	−	−	−	−	−	−	+	−	—
Callistemon	5	100	90-115	420-620	5-6	1-3	−	+	+	−	+	−	−	+	−	−	−	−	−	−	−	+	−	0·90-1·22
Calothamnus	2	100	67-70	260-340	5-6	1-(2)	−	+	+	−	+	−	−	+	−	−	−	−	−	−	−	+	+	0·50-0·60
Choricarpia	2	95-100	76-90	500-710	3-4	1-2	−	+	−	+	−	−	−	+	+	−	−	−	−	−	−	+	−	0·98-1·10
Decaspermum	2	100	105	550-660	3-4	1, 3-4	+	−	−	+	−	−	−	+	−	±	−	−	−	−	−	+	−	1·00-1·10
Eucalyptopsis	2	20-40	150-220	580-790	7-12	1-(2)	−	+	−	−	−	−	+	+	−	+	+	−	−	−	−	−		1·05-1·20
Eucalyptus A	150+	100	55-260	310-765	4-6(2) 7-12	1-3 (4)	−	+	−	−	−	−	+	±	−	+	−	−	±	±	−	+	−	0·70-1·40
Eucalyptus B	27	40-60	140-250	490-610	6-12	1-3	−	+	−	−	−	−	+	+	−	+	+	+	−	+	−	+	−	1·00-1·40
Eugenia A	7	100	75-90	440-720	4-5	1, 2-3	+	−	−	+	−	−	−	+	+	−	−	−	−	+	∓	+	±	0·80-1·27
Eugenia B	24	12-76	97-206	650-1090	8-12	1, (2), 3-5	+	−	−	−	−	+	−	−	−	+	+	∓	−	+	−	−	—	1·10-1·90
Syzygium	14																							
Acmena	4	20-70	112-185	630-800	8-12	1, 3-5 (6)	+	−	−	−	−	+	−	−	−	+	+	+	−	−	−	−	−	1·35-1·67
Cleistocalyx	4	25-82	78-174	630-830	8-12	1, 2-3 (4)	+	−	−	−	−	+	−	−	−	+	+	±	−	+	−	−	−	1·30-1·50
Kjellbergiodendron	3	100	160-185	820-990	7-10	1-2	∓	±	−	−	−	+	−	+	−	+	+	±	−	+	−	+	−	1·23-1·68
Kunzea	2	100	65-92	340-450	4-6	1-3	∓	±	−	+	−	−	−	+	−	−	−	−	−	−	±(1)	+	−	0·76-0·82
Leptospermum	7	45-100	63-130	440-630	3-5	1-3 (4)	∓	±	−	+	−	−	−	+	±	−	−	−	−	−	±(1)	+	−	0·80-1·10
Lophomyrtus	3	100	65	680	4-6	1, 2-(3)	+	−	−	−	+	−	−	+	−	−	−	−	−	−	−	+	−	1·03
Lysicarpus	1	100	83	500	3-4	1-(2)	−	+	+	−	+	−	−	+	−	−	−	−	−	−	−	+	−	0·70
Melaleuca	30	90-100	45-180	260-600	3-5 (7)	1-2 (3)	∓	±	+	−	+(3)	−	±	+	±	∓	−	−	−	−	−	+	+	0·43-1·13
Metrosideros	5	90-100	85-190	570-810	5-8	1-2 (3)	+	−	±	−	+	−	−	+	−	−	−	−	−	−	−	+	+	0·90-1·25
Octamyrtus	1	100	150	790	4-6	1, 2-3	+	−	−	+	−	−	−	+	+	+	−	−	∓	−	−	+	−	1·47
Osbornia	1	100	100	600	3-5	1-2	+	−	+	−	+	−	−	+	±	+	−	−	−	−	−	+		
Pilidiostigma	1	100	130	590	4-5	1, 3-5	+	−	−	+	−	−	−	+	−	−	−	−	−	−	−	+	−	1·21
Piliocalyx	1	25	150	760	8-10	1, 3-4	+	−	−	−	−	+	−	−	−	+	+	+	−	+	−	−	−	1·49
Rhodamnia	6	90-100	88-145	470-780	3-5	1, 3-6 (8)	+	−	−	+	−	−	−	+	±	±	−	−	±	∓(4)	−	+	−	1·20-1·40
Rhodomyrtus	4	95-100	98-127	630-880	4-5	1, 3 (4)	+	−	−	+	−	−	−	+	∓	−	−	−	−	∓(5)	−	+	+	1·20-1·60
Spermolepis	1	100	214	660	7-12	1-2	−	+	−	−	−	−	+	+	∓	+	+	−	−	−	−	+	+	1·30
Syncarpia	2	100	127-145	650-810	5-7	1-2	−	+	+	−	+	−	−	+	−	∓	−	−	±	−	−	+	+	1·14-1·34
Tristania	10	100	72-200	480-860	5-7	1-2	−	+	+	−	+	−	−	+	∓	∓	−	−	∓	−	−	+	+	0·96-1·28
Xanthomyrtus	2	55	102-122	850-960	5-6	1, 3-5	+	−	−	−	+	−	−	+	±	∓	−	−	−	−	−	−	+	1·55-1·69
Xanthostemon	7	100	85-178	620-880	4-7	1-2	−	+	+	−	+	−	−	+	+	—	−	−	−	−	−	+	+	1·00-1·35

∓Minority of species conforming.

± Majority of species conforming.

†E.g. 1, 2-3(4) = uniseriate and 2-3 seriate, occasionally up to 4.

(1) Present in *A. flexuosa*, *K. peduncularis*, *L. ericoides*, and *L. scoparium*.

(2) In *E. salubris*.

(3) In *M. leucadendron* and varieties the vessel-ray pits approach the 'eucalypt' type in size.

(4) Present in *R. cinerea* only.

(5) Present in *R. macrocarpa* only.

tion. These species are not generally considered of commercial importance owing to their poor form and the presence of large pockets of gum and concentric gum veins; when free of these the timbers are sometimes utilized for wheelwrights' work and for fence posts. The heartwood is pinkish brown to red-brown, moderately coarse-textured and generally interlocked in the grain; moderately heavy to heavy, and hard.

(ii) *Structure.—Growth rings* not distinct. *Vessels* intermediate in size and visible to the naked eye; maximum tangential diameters 190-210 μ; mean member length 370-580 μ; not always distinct owing to the presence of abundant tyloses; moderately numerous, 5-10/sq. mm; evenly distributed with occasionally a tendency to oblique arrangement in a few samples; from 30-60 per cent. solitary in different species and samples, remainder generally in radial multiples of 2-4 but sometimes up to 9; vessel pitting coarse, bordered, alternate, vestured, diameter 8-12 μ; perforation plates simple; tyloses abundant. *Vasicentric tracheids* present. *Rays* uni- or biseriate, occasionally triseriate, weakly heterogeneous, the marginal cells tending to be of greater vertical dimensions than the central procumbent cells; maximum height 16-25 cells; vessel-ray pitting large, of the eucalypt type, half-bordered, the apertures coinciding with the border, rounded to irregular in shape (Plate 8, Fig. 4); deposits of extraneous material abundant; crystals and silica absent. *Parenchyma* abundant, paratracheal, vasicentric to aliform, frequently in irregular, loose bands, variable in width and spacing, sometimes up to 12 cells wide; also apotracheal, diffuse, sparse to abundant in the different specimens examined; crystals sparse in *A. cordifolia* to abundant in remainder, solitary or aggregated in individual parenchyma cells and in chambered cells of strand; individual parenchyma cells distinctive in transverse sections owing to their large size. *Fibres* moderately thin to thick-walled, non-septate; with numerous distinctly bordered pits, mean length 0.70-1.20 mm.

(iii) *Material.—Angophora bakeri* E. Cuthbert Hall, three samples eastern Australia; *A. cordifolia* Cav., two samples eastern Australia; *A. costata* (Gaertn.) Britt., one sample Melbourne Botanic Gardens; *A. intermedia* DC., five samples eastern Australia; *A. lanceolata* Cav., 10 samples north-eastern Australia; *A. subvelutina* Cav., three samples north-eastern Australia; *A. woodsiana* F. M. Bail., one sample north-eastern Australia.

(*c*) *Austromyrtus*

(i) *General.*—This genus, described by Burret (1941*b*), contains some 25, and possibly additional species, formerly placed in *Myrtus* Niedenzu and *Eugenia* L. They occur in north-eastern Australia and New Caledonia; samples from three Australian species were available for examination; the heartwood of these species is pink to red-brown or definite brown; fine, uniform-textured, and moderately dense; not of commercial importance.

(ii) *Structure.—Growth rings* poorly to well defined by bands of denser late wood fibres. *Vessels* small and invisible to indistinct to the naked eye, often indistinct even with lens; maximum tangential diameters 48-115 μ; mean member length 620-800 μ; evenly distributed, almost entirely solitary; tending to be rounded; numerous, more than 20/sq. mm; vessel pitting sparse, small, bordered, vestured; diameter 4-6 μ; perforation plates simple. *Vasicentric tracheids* present. *Rays* tending to be of two distinct widths; uniseriate composed of upright cells; multiseriate 3-4, occasionally up to 5, cells wide, composed of procumbent cells with uniseriate margins of square to upright cells, frequently disjunctive; vessel-ray pitting small, half-bordered, and similar to vessel type; extraneous material abundant. *Parenchyma* variable, mainly apotracheal, diffuse tending to short tangential lines; sometimes limited to vicinity of vessels, confined to the abaxial side, and extended into tangential wings; no crystals observed. *Fibres* thick-walled, non-septate, with numerous small but distinctly bordered pits on all walls; mean length 1.15-1.55 mm.

(iii) *Material.—Austromyrtus* sp. aff. *A. acmenioides* (F. Muell.) Burret, two samples north-eastern Australia; *Austromyrtus* sp. (*Eugenia dallachiana* F. Muell.), three samples north-eastern Australia; *A. hillii* (Benth.) Burret, four samples north-eastern Australia.

(iv) *Remarks.*—Two species, *Austromyrtus horizontalis* Burret (*Eugenia horizontalis* (Panch. ex Brongn. & Gris.)) and *Austromyrtus stricta* Burret (*Eugenia stricta* (Panch. ex Brongn. & Gris.)), have been placed by Burret in this genus, but, from the sparse material available for examination, they agree more closely, on wood anatomy, with *Eugenia* (sens. str.) than with *Austromyrtus.*

(*d*) *Backhousia*

(i) *General.*—A genus of seven species of medium-sized to occasionally large trees occurring in north-eastern Australia; specimens of four species were available for examination. The leaves of one species, *B. citriodora*, yield citral commercially. The heartwood of these timbers is very dense, brown to reddish brown in colour, fine and even-textured; used locally for mallets, small tool handles, and turnery.

(ii) *Structure.—Growth rings* not visible to sometimes just visible. *Vessels* small, entirely solitary, rather uneven in size and distribution; maximum tangential diameters 85-175 μ; mean member length 530-780 μ; moderately numerous to very numerous (5-25/sq. mm); sometimes tending to be tangentially zonate or occasionally oblique; oval in shape with the longer axis radial; vessel pitting loosely arranged, small, bordered, vestured; diameter 4-8 μ; perforation plates simple. *Vasicentric tracheids* present. *Rays* mainly uni- or biseriate, occasionally triseriate, almost homogeneous to weakly heterogeneous with 1 to several rows of square or brick-shaped cells greater in vertical dimension than the procumbent, occasionally 1 row of upright cells present; maximum height 25 cells; vessel-ray pitting small, half-bordered, and similar to vessel pitting; deposits of extraneous material abundant; crystals and silica not observed. *Parenchyma* generally apotracheal, diffuse, with a tendency to link up in short discontinuous lines, occasional bands of 2-3 cells present but these are short and discontinuous (Plate 3, Fig. 1); paratracheal parenchyma sparse to absent, where present limited to the abaxial side of vessels; crystal strands observed in *B. bancrofti*; deposits of extraneous material abundant. *Fibres* thick-walled, non-septate; pits small but distinctly bordered, numerous on tangential and radial walls; mean length 0.85-1.55 mm.

(iii) *Material.—Backhousia bancrofti* Bail. & F. Muell., four samples eastern Australia; *B. citriodora* F. Muell., two samples eastern Australia; *B. hughesii* C. T. White, two samples north-eastern Australia; *B. myrtifolia* Hook. & Harv., 12 samples eastern Australia.

(*e*) *Baeckia*

(i) *General.*—A genus of 60 species of small or medium-sized shrubs mainly confined to Australia, but with a few species extending to New Caledonia, and one or two others, extra-Australian, which extend to Indo-Malaya and south China; none of commercial importance. One species was available for examination and this was only from a small stem.

(ii) *Structure.—Growth rings* marked faintly by bands of denser fibres. *Vessels* small and invisible to the naked eye; maximum tangential diameter 72 μ; member length 550 μ; solitary and evenly distributed; perforation plates simple; vessel pitting small, bordered, vestured, diameter 4-6 μ. *Vasicentric tracheids* present. *Rays* uni- or biseriate, weakly heterogenous with many rows of square to upright marginal cells, the procumbent central cells differing little from the adjacent marginal cells which are frequently disjunctive; vessel-ray pitting small, half-bordered, and similar to vessel type; no silica or crystals observed. *Parenchyma* apotracheal diffuse, moderately abundant, often located near the pores; no crystals observed. *Fibres* thick-walled, non-septate with small distinctly bordered pits.

(iii) *Material.—Baeckia virgata* Andrews, one sample eastern Australia.

(*f*) *Callistemon*

(i) *General.*—A genus of 12 species of shrubs or small trees confined to Australia; samples from five species were available for study. The heartwood is light brown to brown, moderately light to moderately heavy, fine and even-textured, hard to cut across the grain; not of commercial importance.

(ii) *Structure.—Growth rings* well defined by variation in fibre wall thickness. *Vessels* small and indistinct to the naked eye; maximum tangential diameters 90-115 μ; mean member length 420-620 μ; evenly distributed with slight tendency to oblique arrangement; moderately numerous to numerous, 9-15/sq. mm; entirely solitary, oval in shape with longer axis radial; vessel pitting sparse, small, bordered, vestured, diameter 5-6 μ; perforation plates simple. *Vasicentric tracheids* present. *Rays* 1-3-seriate, weakly heterogeneous with 1 to several rows of square to upright cells; maximum height 15-20 cells; pits between ray cells numerous on all walls; vessel-ray pits small, half-bordered, apertures almost coinciding with border; resinous deposits abundant in all cells; crystals absent; siliceous inclusions present, mainly in central ray cells. *Parenchyma* apotracheal diffuse, sparse to moderately abundant; no crystals observed. *Fibres* moderately thick-walled; non-septate; pits small and distinctly bordered; mean length 0.9-1.22 mm.

(iii) *Material.—Callistemon lanceolatus* DC., one sample north-eastern Australia; *C. paludosus* F. Muell., one sample south-eastern Australia; *C. rugulosus* DC., one sample south-eastern Australia; *C. salignus* DC., two samples eastern Australia; *C. viminalis* (Gaertn.) Cheel, one sample north-eastern Australia.

(g) *Calothamnus*

(i) *General.*—A genus of some 25 species of shrubs or small trees occurring in Western Australia; two species were available for examination. The heartwood is dark reddish brown in colour; moderately heavy to heavy, fine and even-textured; the trees are too small to be of commercial importance.

(ii) *Structure.—Growth rings* sometimes visible because of a denser band of late wood fibres or a slight variation in size of vessels, or both. *Vessels* almost entirely solitary, extremely numerous, small, even in distribution but variable in size; maximum tangential diameter of largest 70 μ; mean member length short, 260-340 μ; generally oval in shape with the longer axis radial; vessel pitting small, bordered, vestured, diameter 5-6 μ; perforation plates simple; tyloses infrequent. *Vasicentric tracheids* present. *Rays* uniseriate to partly biseriate, maximum height up to 15 cells, weakly heterogeneous, procumbent cells being almost square; cells thick-walled with numerous pits, frequently tending to be disjunctive in the marginal cells which are sometimes vertically elongated; vessel-ray pitting half-bordered, the borders tending to coincide with the aperture and appearing simple, approximately the same size as the vessel pits; deposits of silica present, sparse to abundant, generally associated with resinous material in the central cells of the ray. *Parenchyma* apotracheal, diffuse, sparse to moderately abundant; crystals not observed; deposits of extraneous material abundant. *Fibres* thick-walled, non-septate, with small but distinctly bordered pits; mean length, 0.5-0.6 mm.

(iii) *Material.—Calothamnus gilesii* F. Muell., one sample Western Australia; *C. quadrifidus* R. Br., one sample Western Australia.

(h) *Choricarpia*

(i) *General.*—A small genus of trees confined to eastern Australia; two species were available for examination, these were formerly assigned to the genus *Syncarpia.* The heartwood is pinkish or greyish to red-brown, moderately heavy to heavy, fine and even-textured; not of commercial importance, except in small dimensions for mallets and chisel handles.

(ii) *Structure.—Growth rings* not conspicuous, sometimes discernible because of bands of radially flattened fibres. *Vessels* small and indistinct to the naked eye; maximum tangential diameter 76-90 μ; mean member length 500-710 μ; predominantly to exclusively solitary; numerous, more than 20/sq. mm; tending to be arranged obliquely or in oblique flares (Plate 4, Fig. 2); vessel pitting small, bordered, vestured; diameter 3-4 μ; perforation plates simple; deposits of extraneous material common; white or grey deposits observed in *C. subargentea.* *Vasicentric tracheids* present. *Rays* uni- or biseriate, up to 20 cells high, weakly heterogeneous with 1 to several rows of squarish cells; vessel-ray pitting similar to vessel type, small, half-bordered; deposits of extraneous material abundant; no crystals or silica observed. *Parenchyma* apotracheal, moderately abundant, mainly diffuse in *C. subargentea* with some tendency to form discontinuous narrow bands; bands more numerous and wider in *C. leptopetala*; crystals not observed. *Fibres* thick-walled, non-septate, with numerous distinctly bordered pits; mean length 0.98-1.10 mm.

(iii) *Material.—Choricarpia leptopetala* (F. Muell.) Domin, two samples eastern Australia; *C. subargentea* (C. T. White),* three samples eastern Australia.

(*i*) *Decaspermum*

(i) *General.*—A genus of 24 species, occurring from India, the Malayan region to the Philippines, New Guinea, and north-eastern Australia to Fiji; *D. paniculatum,* one of the two species available for examination, has a wide distribution; in Malaya and the Philippines it occurs only as a shrub or small tree but in Queensland the tree attains a height of more than 100 ft. The heartwood is pink to reddish brown, moderately hard and heavy. It is used locally for tool handles, posts, etc.

(ii) *Structure.—Growth rings* indistinct. *Vessels* small and indistinct to the naked eye; maximum tangential diameter 105 μ; mean member length 550-660 μ; moderately numerous to numerous, 11-16/sq. mm; almost exclusively solitary, evenly distributed and variable in size, generally oval in shape with the longer axis radial; vessel pitting small, bordered, vestured, diameter 3-4 μ; perforation plates simple. *Vasicentric tracheids* present, sparse. *Rays* tending to be of two widths; uniseriate numerous, generally very low (up to 6 cells) composed entirely of upright cells; multiseriate 3-4 cells wide, up to 50 cells high, heterogeneous with 1 to several rows of upright cells; vessel-ray pitting half-bordered and similar to the vessel pitting; deposits of extraneous material abundant; crystals and silica deposits wanting. *Parenchyma* very variable in amount, apotracheal, diffuse, from sparse to abundant, with some paratracheal, incompletely vasicentric. *Fibres* moderately thick-walled, non-septate; pits numerous and distinctly bordered; mean length 1.0-1.1 mm.

(iii) *Material.—Decaspermum neurophyllum* Laut. & Schum., one sample New Guinea; *D. paniculatum* (Lindl.) Kurz (syn. *D. fruticosum* Forst.), one sample north Queensland, five samples New Guinea.

(*j*) *Eucalyptopsis*

(i) *General.*—A recent genus (White 1951), so far containing two species occurring in New Guinea and the Moluccas. Material representing both species was available for examination; the heartwood of these timbers is pinkish to red-brown; moderately fine-textured; grain straight to somewhat interlocked; light to moderately heavy.

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* This species has not yet been transferred to *Choricarpia* but the late Mr. C. T. White in a personal communication agreed to the validity of the transfer.

(ii) *Structure.*—*Growth rings* moderately well defined in the majority of samples by somewhat thicker-walled fibres. *Vessels* small to intermediate in size and visible to the naked eye; maximum tangential diameter 150-220 μ; mean member length 580-790 μ; varying from 20-40 per cent. solitary, the remainder in radial and oblique multiples of 2 or 3, occasionally up to 4, with a few clusters; perforation plates simple; vessel pitting moderately coarse, bordered, alternate, vestured; diameter 7-12 μ; tyloses abundant. *Vasicentric tracheids* absent. *Rays* generally uniseriate (up to 70 per cent.) to partly biseriate (up to 45 per cent. in one sample) (Plate 10, Fig. 3); weakly heterogeneous with at least 1 row of upright cells and 1 to several rows of squarish cells at margins of rays; many uniseriate rays composed of square to upright cells; low, maximum height up to 15 cells; vessel-ray pitting coarse, half-bordered, with wide aperture and narrow border, and appearing simple, rounded to oval and generally vertically elongated; deposits of extraneous material abundant throughout ray cells in most samples; no silica or crystals observed. *Parenchyma* predominantly paratracheal, varying from incompletely vasicentric (Plate 10, Fig. 1) to abundant paratracheal, aliform to confluent (Plate 10, Fig. 2); apotracheal varying from sparse to moderately abundant, diffuse in a few samples; no crystals or silica observed. *Fibres* thin to moderately thick-walled, nonseptate with simple to indistinctly bordered pits, few and inconspicuous; mean length 1.05-1.20 mm.

(iii) *Material.*—*Eucalyptopsis papuana* C. T. White, seven samples Boeroe Is., Moluccas, and eastern New Guinea; *Eucalyptopsis* sp. aff. *E. papuana* C. T. White, one sample Dutch New Guinea.

(*k*) *Eucalyptus*

(*i*) *General.*

A genus of over 600 species and varieties (Blakely 1934) of small to very large trees practically confined to Australia; one species, *E. deglupta* Bl., is not found in Australia and occurs from New Guinea to the Philippines; a few of the Australian species are found in Timor or New Guinea. Many species produce timbers of commercial importance and certain of these have for this reason been planted in many parts of the world. The trees are mainly straight with cylindrical boles and with comparatively small or no buttresses; some of the smaller drier-country species, however, grow characteristically in what is called "mallee" form (producing a large woody mass below ground-level from which arise several small stems). The eucalypt timbers have been broadly classified on bark and wood characteristics and on the essential oil content of the leaves etc., and there are many referencees in Australian forestry literature to such groupings as the stringybarks, ironbarks, boxes, peppermints, gums, bloodwoods, and ashes, etc. The wood anatomy, however, does not always follow such groupings, although in general, the anatomy does fit fairly well Blakely's classification based on anther characteristics.

The sapwood in all species is comparatively narrow, generally less than 1 in. in width, pale in colour; the heartwood is variable in colour from pale brown to deep red-brown, or sometimes chocolate-brown as in *E. microtheca* (coolabah); usually all are rather dense, varying from 40 to 70 lb/cu. ft air dry (*E. microtheca* sometimes up to 80 lb/cu. ft); texture fine to coarse, although the majority are moderately coarse; grain characteristically interlocked; gum veins are a prominent feature of most of the genus. The genus is not entirely homogeneous anatomically; it is possible to divide it into two groups, chiefly on the presence or absence of pore multiples; the anatomical features of each of these are set out below.

(ii) *Structure*

Eucalyptus A.—*Growth rings* generally indistinct in the majority of species; very distinct in *E. gigantea*, *E. pauciflora*, and *E. dalrympleana* where marked by a distinct band of dense late wood fibres usually with few and smaller pores, in *E. gigantea* often the early wood fibres are without pores at the commencement of the growth ring (Plate 6, Fig. 6); less distinct in *E. regnans*, *E. obliqua*, and others of the south-eastern Australian highlands. *Vessels* variable in size from very small (invisible without lens) to large and distinct to the naked eye; maximum tangential diameters from 55 μ in *E. salubris* to 260 μ in *E. deglupta*; member length moderately short (310 μ) to medium-sized (765 μ); evenly distributed in most species with some few exceptions, e.g. *E. gigantea*; entirely solitary but showing varying degrees of oblique arrangement (Plate 5, Figs. 3, 4, and 5); perforation plates exclusively simple, mainly horizontal; vessel pitting generally coarse, bordered, vestured, diameter varying from 4-6 μ in *E. salubris* to 7-12 μ in the remainder; tyloses commonly present. *Vasicentric tracheids* present, often abundant (Plate 7, Fig. 4). *Rays* 1-3-seriate, occasionally up to 4; generally less than 20 cells high; weakly heterogeneous with 1 to several rows of procumbent cells of greater vertical dimensions than the central cells; vessel-ray pitting large, half-bordered but with large, rounded to oval apertures almost coinciding with the border (Plate 8, Fig. 6); kino-like deposits usually abundant, sometimes segregated into the central procumbent cells; crystals and siliceous inclusions absent. *Parenchyma* of two types, apotracheal and paratracheal; paratracheal varying from a few cells in contact with the vessels as in *E. paniculata* to abundantly vasicentric as in *E. goniocalyx* (Plate 5, Fig. 3); apotracheal rare in many species, in others abundantly diffuse; kino-like deposits common in the red coloured timbers, crystal strands and chambered crystals present chiefly in the boxes, gums, and ironbarks; siliceous inclusions not observed. *Fibres* medium to thick-walled, non-septate, with conspicuously bordered pits; mean length in mature wood varies from 0.70 mm in *E. hemiphloia* to 1.40 mm in *E. diversicolor*.

Eucalyptus B.—(The timbers listed under the *Corymbosae Non-Peltatae* and *Corymbosae-Peltatae*, of Blakely's classification, have been considered under this section; these groups are generally known as the bloodwoods and include the spotted gums.)

These timbers can be separated anatomically from others of the genus *Eucalyptus* by two features, the arrangement of the vessels and the parenchyma distribution. Whereas the majority of the eucalypts have solitary vessels, in this group there is a definite tendency for many of the vessels to be in short to long radial multiples and sometimes in clusters (Plate 5, Fig. 2); in addition, the parenchyma is usually abundant, paratracheal, vasicentric to aliform and confluent, and diffuse; the aliform to confluent arrangement is not found in other species of *Eucalyptus* and is characteristic of this group. In other anatomical features there are no significant differences and the descriptions given for the main group (*A*) of *Eucalyptus* hold. The timbers of this group are very similar to those of the genus *Angophora* and anatomically it is difficult to distinguish between them (Plate 5, Figs. 1 and 2).

(iii) *Material.*—For determining the anatomy of *Eucalyptus A* material from some 150 species has been examined.

Under *Eucalyptus B* the following species have been examined: *Eucalyptus abbreviata* Blakely & Jacobs, one sample northern Australia; *E. abergiana* F. Muell., one sample north-eastern Australia; *E. calophylla* R. Br., two samples Western Australia; *E. citriodora* Hook., two samples north-eastern Australia; *E. clavigera* A. Cunn., four samples northern Australia; *E. corymbosa* Sm., 27 samples north-eastern Australia; *E. dichromophloia* F. Muell., three samples northern Australia; *E. erythrophloia* Blakely, two samples north-eastern Australia; *E. eximia* Schauer, 10 samples eastern Australia; *E. ferruginea* Schauer, two samples northern Australia; *E. ficifolia* F. Muell., six samples Western Australia; *E. foelscheana* F. Muell., two samples northern Australia; *E. grandifolia* R. Br., two samples northern Australia; *E. haematoxylon* Maiden, 10 samples Western Australia; *E. jacobsiana* Blakely, one sample northern Australia; *E. latifolia* F. Muell., one sample northern Australia; *E. leiophloia* Blakely & Jacobs, two samples northern Australia; *E. maculata* Hook., 44 samples eastern Australia; *E. papuana* F. Muell., three samples northern Australia; *E. peltata* Benth., two samples north-eastern Australia; *E. ptychocarpa* F. Muell., two samples northern Australia; *E. setosa* Schauer, two samples northern Australia; *E. terminalis* F. Muell., four samples northern Australia; *E. tessellaris* F. Muell., five samples north-eastern Australia; *E. torelliana* F. Muell., one sample north-eastern Australia; *E. trachyphloia* F. Muell., four samples north-eastern Australia.

(*l*) *Eugenia A*

Eugenia (sens. lat.) has been subdivided into two main groups on anatomical grounds:

(1) *Eugenia A.*—Timbers characterized by the presence of vasicentric tracheids and fibre tracheids and by solitary pores, apotracheal parenchyma, and vessel-ray pitting small and similar to the vessel type, and

(2) *Eugenia B.*—Timbers characterized by the absence of vasicentric tracheids and fibre tracheids and by the presence of multiples of pores,

paratracheal parenchyma, and coarse, apparently simple, to scalariform vessel-ray pitting.

Species placed in *Acmena* and *Cleistocalyx* are anatomically very similar to *Eugenia B,* therefore descriptions for these two follow that of *Eugenia B.*

(i) *General—Eugenia* (sens. str.) comprises a large number of trees and shrubs, with a few species of commercial size, distributed abundantly throughout tropical and subtropical America, but sparingly in the area under consideration. The timbers are not of commercial importance. Heartwood brown to red-brown, moderately heavy to heavy; fine-textured.

(ii) *Structure.—Growth rings* not distinct, sometimes apparently marked by bands of parenchyma and sometimes by bands of fibres without parenchyma or pores. *Vessels* small and indistinct to the naked eye; maximum tangential diameter 75 μ (*E. grisiana*) to 90 μ (*E. salomonica*); mean member length 440 μ (*E. grisiana*) to 720 μ (*E. salomonica*); solitary, oval in shape with either radial or sometimes tangential axis elongated, variable in size; vessel pitting sparse, small, bordered, vestured; diameter 4-5 μ; perforation plates simple. *Vasicentric tracheids* present. *Rays* 1-3-seriate, typically heterogeneous with several rows of upright cells; ray cells thick-walled and abundantly pitted, upright cells frequently disjunctive; vessel-ray pitting small, half-bordered, and similar to vessel type; deposits of extraneous material abundant; no crystals or silica observed. *Parenchyma* apotracheal, abundant, chiefly in fine, numerous, sometimes discontinuous lines, mainly uniseriate, sometimes diffuse; crystal strands common, large crystals sometimes present. *Fibres* thick-walled, non-septate, with numerous distinctly bordered pits; fibre length 0.80 mm (*E. grisiana*) to 1.27 mm (*E. salomonica*).

(iii) *Material.—Eugenia carissoides* F. Muell., (H)* one sample north-eastern Australia; *E. gacognei* Montr., (H) one sample New Caledonia; *E. grisiana* Guill., one sample New Caledonia; *E. horizontalis* Panch., (H) one sample New Caledonia; *E. macrohila* C. T. White & Francis, (H) one sample north-eastern Australia; *E. salomonica* C. T. White, one sample Solomon Is.; *E. stricta* Panch., (H) one sample New Caledonia.

For comparison with the above species from the area under consideration, the following species from the New World and from Africa were also examined: *Eugenia axillaris* Koord. and Val., W. Indies and tropical America, one sample; *E. cartagensis* Berg., Costa Rica, one sample; *E. confusa* DC., W. Indies and tropical America, one sample; *E. cotinifolia* Jacq., Mauritius, one sample; *E. origanoides* Berg., British Honduras, one sample; *E. stockii* Standl., Costa Rica, one sample; *E. uniflora* L., tropical America, one sample; *E. valerii* Standl., Costa Rica, one sample.

The same structure, with minor differences in the parenchyma distribution, was observed. In some species the apotracheal parenchyma tended to be in bands up to 6 cells wide as well as in discontinuous uniseriate lines. Parenchyma strands containing chambered crystals were observed in *E. stockii*; in the other species, with the exception of *E. valerii*, where no crystals were observed, enlarged crystal-bearing cells were present, sometimes solitary, but more often in longitudinal series of 2 to several, commonly 2-4.

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* (H) signifies twig material from herbarium specimens only.

(*m*) *Eugenia B*

(i) *General.*—Included under this description are species from the genera *Eugenia* (excluding *Eugenia A* above) and *Syzygium*. These genera have a large number of species and are confined to the tropics of the Old World, chiefly Asia, Malaysia, Australia, New Zealand, New Guinea, and islands of the Pacific. Many of the species produce trees of merchantable size, notably *E. francisii*, rose satinash, commercially important in Australia, and many of the species of *Syzygium* from New Guinea and the Solomon Is. are large first-storey trees which should produce merchantable timber for general construction and interior finish; the heartwood is pale brown to brown or grey-brown, sometimes reddish brown in colour, moderately heavy.

(ii) *Structure.*—*Growth rings* not marked. *Vessels* small and indistinct to the naked eye to moderately large and distinct to the naked eye; maximum tangential diameters 100-200 μ; mean member length 650-1,090 μ; moderately to very numerous, numbering 6 to more than 20/sq. mm; evenly distributed; 12-76 per cent. solitary, and in radial multiples of 2-8, majority up to 4 or 6, some clusters; vessel pitting medium-sized, bordered, alternate, vestured; diameter 8-12 μ; perforation plates simple; tyloses and deposits sparse. *Vasicentric tracheids* absent. *Rays* 1-5-seriate, with some tendency to be of two widths (Plate 9, Fig. 2); uniseriate entirely of upright cells, multiseriate heterogeneous with uniseriate margins of 1 to many rows of upright cells; maximum height varying from 20 to 50 cells; vessel-ray pitting half-bordered, but apparently simple, rounded to elongated, either vertically or obliquely and in scalariform arrangement (Plate 8, Fig. 3), sometimes unilaterally compound; deposits of extraneous material abundant; no silica or crystals observed. *Parenchyma* paratracheal, variable in amount, completely or incompletely vasicentric (Plate 2, Fig. 6), to aliform and confluent, sometimes forming wavy, irregular, and discontinuous bands 2-5 cells wide and occasionally in very regular continuous bands up to 6 or more cells wide (Plate 2, Fig. 4), crystal strands present (Plate 9, Fig. 4) or absent in different species, when present, either chambered or solitary; no silica observed; deposits of extraneous material present. *Fibres* medium to thick-walled, non-septate; pits inconspicuous and indistinctly bordered; length 1.10-1.90 mm. Patches of included bark large and of regular occurrence in *E. angophoroides, E. jambosoides, E. bleeseri*, and *E. suborbicularis*.

(iii) *Material.*—*Eugenia angophoroides* F. Muell., one sample north-eastern Australia; *E. bleeseri* Schwarz in Fedde, one sample northern Australia; *E. clusiaefolia* A. Gray, two samples Solomon Is.; *E. cormiflora* F. Muell., two samples north-eastern Australia; *E. corynantha* F. Muell., six samples north-eastern Australia; *E. corrugata* King, one sample Malaya; *E. crebrinervis* C. T. White, three samples eastern Australia; *E. erythrocalyx* C. T. White, one sample north-eastern Australia; *E. fastigata* (Bl.) Koord. & Valet., one sample North

Borneo; *E. francisii* Bail., seven samples north-eastern Australia; *E. frutesceus* (Brongn. & Gris.) Benth. & Hook., one sample New Caledonia; *E. jambolana* Lam., three samples Siam, India, and northern Australia; *E. johnsonii* F. Muell., one sample north-eastern Australia; *E. kuranda* F. M. Bail., one sample north-eastern Australia; *E. leptantha* Wight, two samples north-eastern Australia; *E. luehmanii* F. Muell., two samples north-eastern Australia; *E. maire* A. Cunn., two samples New Zealand; *E. penangiana* Duthie, one sample Malaya; *E. punctulata* Bail., one sample north-eastern Australia; *E. suborbicularis* Benth., two samples north-eastern Australia; *E. valdevenosa* Duthie, one sample North Borneo; *E. ventenatii* Benth., two samples north-eastern Australia; *E. virens* (Bl.) Koord. & Valet., one sample North Borneo; *E. wilsoni* F. Muell., one sample north-eastern Australia.

Syzygium buettnerianum (K. Schum.) Niedenzu, five samples New Guinea; *S. clavatum* (Korth.) Merr. & Perry, one sample North Borneo; *S. decipiens* (Koord. & Val.) Merr. & Perry, one sample Solomon Is.; *S. effusum* (A. Gray) C. Muell., one sample Solomon Is.; *S. grande* Walp., two samples Malaya and northern Australia; *S. jambosoides* (Lauterb.) Merr. & Perry, five samples northern Australia; *S. lateriflorum* Brongn. & Gris., one sample New Caledonia; *S. micrandrum* Merr. & Perry (net. L. M. Perry), one sample Solomon Is.; *S. muelleri* Miq. (=*Eugenia venulosa* Wall.), one sample Malaya; *S. nutans* (K. Schum.) Merr. & Perry, one sample Solomon Is.; *S. paniculatum* Gaertn. (=*Eugenia australis* Wendl. and *E. myrtifolia* Sims), six samples north-eastern Australia; *S. papuasicum* (Bl.) Merr. & Perry, four samples New Guinea; *S. samarangense* (Bl.) Merr. & Perry, one sample Solomon Is.; *S. subcorymbosum* Merr. & Perry, two samples New Guinea; *S. walkeri* Merr. & Perry, one sample Solomon Is.

Acmena

(i) *General.*—Under this grouping are 11 named species of small to large trees, extending from Burma, Siam, and southern China through Malaysia and the Philippines to northern and eastern Australia and the Solomon Is. Samples from four species were available for study. Three of the Australian representatives were formerly included under the genus *Eugenia* (sens. lat.); two of these, *A. hemilampra*, white Eungella gum, and *A. brachyandra*, red apple, are of commercial importance, the trees attaining a height of over 100 ft. *A. smithii* is usually a smaller tree and not of economic importance. The heartwood is variable in colour from pale brown to grey-brown, occasionally with yellowish tints; moderately light to moderately heavy, texture generally uniform, moderately hard to cut across the grain; used mainly for general house framing and light construction, flooring, etc.

(ii) *Structure.*—*Growth rings* indistinct, occasionally a banded or tangentially zonate arrangement of the pores in some samples gives a false impression of growth rings. *Vessels* small and indistinct to the naked eye (*A. smithii*) to intermediate and visible to the naked eye; maximum tangential diameters varying from 112 to 185 μ; mean member length medium-sized, 630-800 μ; numerous, 12-25/sq. mm, evenly distributed, sometimes tangentially zonate; solitary pores varying from 20 per cent. of total in *A. hemilampra* to 70 per cent. in *A. brachyandra,* remainder of pores in radial multiples of 2-5, sometimes up to 8; perforation plates simple; vessel pitting medium sized, bordered, alternate, vestured; diameter 8-12 μ; tyloses common in *A. smithii,* white deposits generally conspicuous macroscopically in *A. hemilampra. Vasicentric tracheids* absent. *Rays* predominantly 3-5-seriate, sometimes up to 6, tending to be of two distinct widths; uniseriate rays low, up to 15 cells, composed of square to upright cells; the multiseriate heterogeneous with uniseriate margins of several rows of square and upright cells; up to 50 cells high; vessel-ray pitting half-bordered, the apertures large and almost coinciding with the borders, rounded or irregular in shape to frequently gash-like to scalariform, vertically to obliquely oriented, sometimes unilaterally compound; crystals and silica absent; deposits of extraneous material sparse, chiefly in procumbent cells. *Parenchyma* abundant, paratracheal, completely or sometimes incompletely vasicentric, aliform to confluent in narrow to wide, wavy and irregular bands 3-10 cells wide; crystals not observed. *Fibres* non-septate, moderately thick-walled; pits indistinctly bordered and inconspicuous; length 1.35-1.67 mm.

(iii) *Material.—Acmena brachyandra* (Maid. & Betche) Merr. & Perry, three samples eastern Australia; *A. hemilampra* (F. Muell. ex. F. M. Bail.) Merr. & Perry, six samples north-eastern Australia; *A. macrocarpa* C. T. White; two samples north-eastern Australia; *A. smithii* (Poir.) Merr. & Perry, five samples eastern Australia.

Cleistocalyx

(i) *General.*—In this group are 21 named species (possibly others) of medium-sized to large trees occurring from Burma, Siam, and south-eastern China through Malaysia to New Guinea, north-eastern Australia, New Caledonia, and Fiji; formerly ascribed to *Eugenia* (sens. lat.). Samples from four species were available for study. One species is of commercial importance in Australia, namely *C. gustavioides,* grey satinash. Heartwood is light to pinkish brown, sometimes with yellowish tints; moderately light to moderately heavy; uniform in texture; intermediate in hardness to cut across the grain; straight-grained to somewhat interlocked. *C. gustavioides* is used for general light construction, house framing, flooring, and has been found useful as a veneer timber and for furniture. *C. operculatus* is a smaller tree.

(ii) *Structure.—Growth rings* ill-defined but sometimes simulated by a banded or zoned appearance of the pores. *Vessels* small to moderately small and visible to the naked eye; maximum tangential diameters varying from 78 to 174 μ in the different species; mean member length 630-830 μ; numerous to very numerous, 10-25/sq. mm, and evenly distributed, sometimes tending to be tangentially zonate or oblique; solitary and in radial multiples of 2-6 or 8, generally 2-4 with a few clusters; vessel pitting moderately coarse, bordered, alternate, vestured, diameter 8-12 μ; perforation plates exclusively simple; tyloses common to infrequent. *Vasicentric tracheids* absent. *Rays* 1-4-seriate with slight tendency to two widths, heterogeneous, the uniseriate rays composed of squarish or upright cells, the multiseriate with marginal rows of squarish and upright cells; vessel-ray pitting half-bordered, the aperture almost coinciding with the border and appearing simple, rounded to elongated and frequently scalariform in arrangement vertically or obliquely inclined, sometimes unilaterally compound; crystals and silica deposits not observed; deposits of extraneous material frequently abundant. *Parenchyma* paratracheal, aliform to confluent, sometimes forming bands 2-5 cells wide (Plate 2, Figs. 2 and 3); crystals present; deposits of extraneous material sometimes present. *Fibres* moderately thin to thick-walled, non-septate, pits few, inconspicuous, and indistinctly bordered; mean length 1.30-1.50 mm.

(iii) *Material.—Cleistocalyx ellipticus* (A. C. Smith) Merr. & Perry, one sample Fiji; *C. gustavioides* (F. M. Bail.) Merr. and Perry, eight samples northeastern Australia; *C. operculatus* (Roxb.) Merr. and Perry, nine samples northern Australia; *C. seemani* (A. Gray) Merr. and Perry, one sample Fiji.

(*n*) *Kjellbergiodendron*

(i) *General.*—This genus, first described in 1936, consists of three species occurring in the Celebes; five samples of these species were available for examination. The heartwood is pale to dark brown; moderately dense to dense; moderately fine-textured, somewhat interlocked in the grain.

(ii) *Structure.—Growth rings* not evident. *Vessels* intermediate in size, indistinct to visible to the naked eye; maximum tangential diameter 160-185 μ; mean member length 820-990 μ; exclusively solitary, occasionally tending to an oblique arrangement and sometimes zonate showing pored and comparatively poreless tangential zones; few to moderately numerous, 3-8/sq. mm; perforation plates simple, frequently almost horizontal; vessel pitting sparse, moderately coarse, bordered, vestured; diameter 7-10 μ; white deposits often present, visible with hand lens; tyloses present, often abundant. *Vasicentric tracheids* present, not numerous. *Rays* uni- or biseriate, often predominantly uniseriate; up to 25 cells high; weakly heterogeneous to heterogeneous with marginal rows of cells square to more than 3 rows of upright cells; procumbent cells short, brick-shaped; vessel-ray pitting half-bordered but appearing simple with large apertures rounded to vertically or obliquely elongated and tending to scalariform (Plate 10, Fig. 6); extraneous material moderately abundant; no crystals or silica observed. *Parenchyma* moderately abundant to abundant paratracheal, sometimes incompletely vasicentric, but often abundantly aliform and confluent in loose, discontinuous bands (Plate 10, Fig. 5); some diffuse present; strands partly composed of chambered crystal-bearing cells; extraneous material not abundant. *Fibres* thick to very thick-walled, non-septate with numerous distinctly bordered pits on radial and tangential walls; mean length 1.23-1.68 mm.

(iii) *Material.—Kjellbergiodendron celebicum* (Koord.) Merr.,* two samples

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* *Note added in Proof.*—In a recent publication (Van Steenis, C. G. G. J. (1952).—*Kjellbergiodendron* and *Whiteodendron*, Malaysian Myrtaceae — Leptospermoideae, Metrosiderinae. *Acta Bot. Neerl.* 1) it is noted that the three species of *Kjellbergiodendron* have been reduced to *K. celebicum* (Koord.) Merr.

Minahassa and Moena Is., Celebes; *K. hylogeiton* Burret, two samples Malili, Celebes; *K. limnogeiton* Burret, one sample Malili, Celebes.

(*o*) *Kunzea*

(i) *General.*—A small genus of shrubs confined to Australia; samples from small stems of two species were available for examination; wood moderately dense; fine-textured, and pale to red-brown.

(ii) *Structure.*—*Growth rings* moderately defined, pores tending to be zonate in the early wood. *Vessels* small and invisible to the naked eye; maximum tangential diameters 65-92 μ; mean member length 340-450 μ; vessel pitting small, bordered, vestured, diameter 4-6 μ; perforation plates simple. *Vasicentric tracheids* present. *Rays* 1-3-seriate, multiseriate somewhat heterogeneous, grading from short procumbent central cells to several rows of square to upright cells at the margins, often disjunctive; uniseriate rays mainly square to upright; no silica or crystals observed; vessel-ray pits small, half-bordered, and similar to vessel pits. *Parenchyma* apotracheal, diffuse; occasional strands of enlarged crystal-bearing cells observed in *K. peduncularis*. *Fibres* thick-walled, nonseptate, with numerous, distinctly bordered pits on radial and tangential walls; mean length 0.76-0.82 mm.

(iii) *Material.*—*Kunzea ambigua* (Sm.) Druce, two samples eastern Australia; *K. peduncularis* F. Muell., one sample Melbourne Botanic Gardens.

(*p*) *Leptospermum*

(i) *General.*—A genus of shrubs and small trees confined mainly to Australia but a few species occurring in Malaya, Java, New Guinea, and New Zealand. Seven species were available for examination. The genus as a whole is not of commercial importance though occasionally used for small turned articles, golf club heads, and small tool handles. The heartwood is pinkish to red-brown, moderately heavy to heavy, fine and uniform-textured, generally interlocked in the grain.

(ii) *Structure.*—*Growth rings* usually distinct, marked by thicker-walled fibres and fewer pores. *Vessels* small and indistinct to the naked eye; maximum tangential diameters 63-130 μ; mean member length 440-630 μ; numerous to very numerous, 13 to more than 20/sq. mm; in some species entirely solitary, in others varying from 45 to 95 per cent. solitary, the remainder in radial multiples of 2-4, sometimes with a tendency to oblique chains and tangential arrangement in localized areas; vessel pitting small, bordered, alternate, vestured, diameter 3-5 μ; perforation plates simple; white and dark-coloured deposits common in most species. *Vasicentric tracheids* present. *Rays* 1-4-seriate, generally 2-3, up to 30 cells high, uniseriate generally less than 8 cells high; weakly heterogeneous with few rows of square cells of greater vertical dimensions than the central procumbent, to heterogeneous with 1-3 rows of upright cells in 2 species (*L. brachyandrum* and *L. erubescens*); vessel-ray pitting small, half-bordered, and similar to vessel type (Plate 8, Fig. 1); deposits of extraneous material common; no silica or crystals present. *Parenchyma* apotracheal, diffuse, sparse to abundant with a tendency to form discontinuous uniseriate lines; large crystal-bearing cells in vertical series in *L. scoparium* and *L. ericoides* (Plate 9, Fig. 6), absent in the remainder; deposits of extraneous material abundant. *Fibres* medium thick-walled to thick-walled, non-septate, with small, distinctly bordered pits; mean length 0.80-1.10 mm.

(iii) *Material.—Leptospermum brachyandrum* (F. Muell.) Cheel, one sample north-eastern Australia; *L. ericoides* A. Rich., two samples New Zealand; *L. erubescens* Schau., one sample Western Australia; *L. laevigatum* (Gaertn.) F. Muell., one sample South Australia; *L. lanigerum* Sm., two samples Tasmania and eastern Australia; *L. myrtifolium* Sieb., one sample eastern Australia; *L. scoparium* Forst., four samples New Zealand.

(*q*) *Lophomyrtus*

(i) *General.*—This genus, split off from *Myrtus* L. by Burret, is confined to New Zealand and consists of three species of shrubs or small trees rarely exceeding 20 ft; samples from these three species were available for examination. The heartwood is moderately dense, fine, and uniform-textured, and red to red-brown in colour.

(ii) *Structure.—Growth rings* ill-defined to absent. *Vessels* small and indistinct even with lens; maximum tangential diameter 65 μ; mean member length 680 μ; entirely solitary and evenly distributed; numerous, 20 + /sq. mm; perforation plates simple, oblique; vessel pitting small, bordered, vestured, diameter 4-6 μ; tyloses not observed. *Vasicentric tracheids* present, few. *Rays* uni- or biseriate (occasionally triseriate); heterogeneous; uniseriate all of upright cells, multiseriate of procumbent and upright, often of several rows, often disjunctive; up to 25 cells high; vessel-ray pitting small, rounded to elongated, apparently simple; extraneous material abundant; no silica or crystals observed. *Parenchyma* apotracheal, diffuse, extraneous material abundant; no silica or crystals observed. *Fibres* thick-walled, non-septate with numerous distinctly bordered pits on radial and tangential walls; mean length 1.03 mm.

(iii) *Material.—Lophomyrtus bullata* Burret, one sample New Zealand; *L. obcordata* (Raoul) Burret, one sample Melbourne Botanic Gardens; *L. ralphii* (Hook. f.) Burret, one sample Melbourne Botanic Gardens.

(*r*) *Lysicarpus*

(i) *General.*—A monotypic genus occurring in north-eastern Australia. *L. angustifolius* is a small tree up to 20 ft high, not common or of commercial importance; the heartwood is reddish brown, fine and uniform-textured, moderately heavy to heavy, said to be durable in the ground and to be termite resistant.

(ii) *Structure.—Growth rings* ill-defined. *Vessels* small and indistinguishable to the naked eye; maximum tangential diameter 83 μ; mean member length 500 μ; exclusively solitary, variable in size, rounded; very numerous, more than 20/sq. mm; vessel pitting fine, bordered, vestured; diameter 3-4 μ; perforation plates simple; tyloses moderately abundant. *Vasicentric tracheids* present. *Rays* mainly uniseriate to sometimes biseriate in part; low, maximum height 15 cells; weakly heterogeneous with marginal cells of slightly greater vertical dimensions than the procumbent; vessel-ray pitting small, half-bordered, with narrow border and appearing simple, round to sometimes elongated; siliceous inclusions abundant in central ray cells; no crystals observed. *Parenchyma* sparse, diffuse; deposits of extraneous material infrequent; no crystals observed. *Fibres* medium thick-walled, non-septate; pits numerous on both tangential and radial walls, distinctly bordered; length 0.70 mm.

(iii) *Material.—Lysicarpus angustifolius* (Hook.) Druce (= *L. ternifolius* F. Muell.), one sample north-eastern Australia.

(*s*) *Melaleuca*

(i) *General.*—A large genus of shrubs and small trees occurring chiefly in Australia, two species occurring in New Caledonia and *M. leucadendron,* a polymorphic species with several varieties which extends from northern Australia to New Guinea, New Caledonia, the Philippines, and Malaya; the bark of most species is flaky and papery; the timbers of some species are used for small turned articles, golf club heads, and tool handles; the leaves of *M. leucadendron* are the source of cajeput oil. The heartwood is pale brown to reddish brown in colour, sometimes with greyish tinge; moderately light to heavy; generally fine-textured; straight or interlocked in the grain.

(ii) *Structure.—Growth rings* usually marked by thicker-walled, radially flattened fibres with sometimes a tendency for the pores to be fewer and smaller in the late wood. *Vessels* vary from extremely small and indistinguishable to the naked eye to visible to the naked eye; maximum tangential diameters 45-180 μ; mean member length 260-600 μ; moderately numerous to numerous, varying from 5 to more than 20/sq. mm; evenly or unevenly distributed, sometimes tending to a tangentially zonate or an oblique arrangement; almost entirely solitary (90-100 per cent.); vessel pitting small, bordered, vestured, diameter 3-5 μ; perforation plates simple; tyloses and white deposits present in some species. *Vasicentric tracheids* present in all species. *Rays* 1-3-seriate, mainly 1-2, or up to 90 per cent. uniseriate in several species; maximum height generally under 20 cells, occasionally up to 25 cells; weakly heterogeneous to heterogeneous; in species with the narrower rays the cells tend to be mainly brick-shaped to squarish or occasionally upright on the margins; in those with wider rays there is a more marked distinction between central procumbent and marginal cells; vessel-ray pitting half-bordered, but appearing simple, rounded to sometimes elongated, variable in size and distinctness between species, largest in *M. leucadendron* (Plate 8, Fig. 7) and varieties; deposits of extraneous material usually abundant; siliceous inclusions present in all species but *M. squarrosa,* in general confined to the central cells of the ray whether procumbent or brick-shaped to square; no crystals observed. *Parenchyma* apotracheal, sparse to abundant, diffuse, sometimes tending to form irregular, short, discontinuous lines, particularly in *M. leucadendron* and varieties; sometimes sparsely paratracheal; deposits of extraneous material common; no silica or crystals observed. *Fibres* moderately thin- to thick-walled; non-septate, with small, distinctly bordered pits; mean length varying from 0.43 to 1.13 mm.

(iii) *Material.**—*Melaleuca acacioides* F. Muell., two samples north-eastern Australia; *M. acuminata* F. Muell., one sample south-eastern Australia; *M. angustifolia* Gaertn., one sample north-eastern Australia; *M. armillaris* Sm., one sample north-eastern Australia; *M. bracteata* F. Muell., one sample north-eastern Australia; *M. cardiophylla* F. Muell., one sample Western Australia; *M. cordata* Benth., one sample Western Australia; *M. coriacea* Poir., three samples eastern Australia; *M. cunninghamii* Schau. ex Walp., one sample northern Australia; *M. eleutherostachya* F. Muell., one sample Western Australia; *M. ericifolia* Sm., four samples eastern Australia; *M. genistifolia* Sm., four samples eastern Australia; *M. glomerata* F. Muell., one sample South Australia; *M. halmaturorum* F. Muell., one sample Western Australia; *M. lasiandra* F. Muell., one sample northern Australia; *M. lateriflora* Benth., one sample Western Australia; *M. leucadendron* L., eight samples northern and north-eastern Australia, New Caledonia; *M. leucadendron* L. var. *lanciifolia* Bail., one sample north-eastern Australia; *M. leucadendron* L. var. *mimosoides* A. Cunn., one sample northern Australia; *M. leucadendron* L. var. *viridis* Salisb., three samples Western Australia; *M. linariifolia* Sm., four samples eastern Australia; *M. macronycha* Turcz., one sample Western Australia; *M. pauciflora* Turcz., one sample eastern Australia; *M. pubescens* Schau., one sample south-eastern Australia; *M. radula* Lindl., one sample Western Australia; *M. squarrosa* Donn. ex Sm., four samples southern Australia; *M. styphelioides* Sm., one sample eastern Australia; *M. thyoides* Turcz., one sample Western Australia; *M. uncinata* R. Br., locality unknown; *M. viridiflora* Gaertn., one sample eastern Australia; *M.* sp. unassigned, one sample Indonesia.

(*t*) *Metrosideros*

(i) *General.*—A widely spread genus occurring from Malaya to New Guinea and northern Australia to New Caledonia, New Zealand, Polynesia, and Hawaii; samples from five species were available for examination; the trees are medium-sized to large; the heartwood is dark in colour, usually red-brown to sometimes purplish brown; heavy to very heavy; fine and uniform-textured; straight-grained or interlocked; some species have a reputation for durability, and are used commercially for posts, stumps, and heavy construction.

* *Note added in Proof.*—Recently two samples of *M. symphyocarpa* F. Muell. have been received; one from Northern Territory, the other from the Oriomo R., southern New Guinea. The secondary wood of these two samples is sufficiently different from that of other species of *Melaleuca* to be worthy of note. It differs mainly in having small, distinctly bordered vessel-ray pits, which are similar to the vessel pits. Other features are the absence of siliceous inclusions in the rays and a ray type which approaches more closely to that of the Myrtoideae section of the family. Examination of twig material also shows the fundamental difference in the vessel-ray pits and this feature alone would indicate some doubt as to its correct placing in *Melaleuca.*

(ii) *Structure.—Growth rings* usually not visible. *Vessels* small and invisible to visible to the naked eye; maximum tangential diameter 85-190 μ; mean member length 570-810 μ; evenly distributed or sometimes tending to be more numerous in the early part of the growth ring; moderately numerous to numerous, 6-11/sq. mm; predominantly to exclusively solitary (90-100 per cent.); vessel pitting small, bordered, vestured, diameter 5-8 μ; perforation plates simple. *Vasicentric tracheids* present. *Rays* 1-3-seriate, generally 2; up to 25 cells high; heterogeneous with 1 to several rows of upright cells at margins (Plate 9, Fig. 1); vessel-ray pitting small, half-bordered, with narrow border, and appearing simple and rounded to sometimes elongated vertically or obliquely; deposits of extraneous material abundant; siliceous inclusions large, abundant to very sparse or absent, confined to central procumbent cells; abundant in *M. ornata* and *M. eucalyptoides,* sparse and small in *M. excelsa* and one sample of *M. robusta,* absent in the remainder. *Parenchyma* chiefly apotracheal, diffuse; deposits of extraneous material abundant. *Fibres* thick-walled, non-septate with numerous small, distinctly bordered pits; mean length 0.9-1.24 mm.

(iii) *Material.—Metrosideros eucalyptoides* F. Muell., one sample northern Australia; *M. excelsa* Soland, one sample New Zealand; *M. ornata* C. T. White, one sample New Guinea; *M. robusta* A. Cunn., three samples New Zealand; *M. lucida* Menzies., two samples New Zealand; *M.* sp. unassigned, one sample northeastern Australia.

(*u*) *Octamyrtus*

(i) *General.*—A small genus of six species (White 1951) occurring in New Guinea and the Moluccas. A sample from one species was available for examination. The heartwood is pinkish brown, moderately heavy; fine and uniform in texture.

(ii) *Structure.—Growth rings* indistinct. *Vessels* small and indistinct to the naked eye to just visible, variable in size; maximum tangential diameter 151 μ; member length 790 μ; entirely solitary; moderately numerous, 7-8/sq. mm; perforation plates simple; vessel pitting alternate, bordered, vestured; diameter 4-6 μ. *Vasicentric tracheids* present. *Rays* uni- or biseriate, occasionally triseriate, uniseriate numerous, composed of upright cells, up to 8 cells high; multiseriate heterogeneous, of procumbent cells with uniseriate margins of upright cells up to 8 in number; vessel-ray pitting half-bordered, small, and similar to vessel pitting; deposits of extraneous material not abundant; no silica or crystals observed. *Parenchyma* moderately abundant, apotracheal, diffuse, tending to link up into short, loose bands, often adjacent to pores; paratracheal, sparse, incompletely vasicentric; no silica or crystals observed. *Fibres* moderately thick-walled, non-septate, with numerous conspicuously bordered pits on radial and tangential walls; mean length 1.47 mm.

(iii) *Material.—Octomyrtus pleiopetala* (F. Muell.) Diels, one sample New Guinea.

(*v*) *Osbornia**

(i) *General.*—A monotypic genus occurring from the Philippines to New Guinea and northern Australia; the species is a small tree occurring at the back of mangrove or littoral associations. The heartwood is dark greyish to reddish brown; fine and uniform-textured, dense, the grain generally wavy and interlocked.

(ii) *Structure.*—*Growth rings* indistinct. *Vessels* small and indistinct to the naked eye; maximum tangential diameter 100 μ; vessel member length 600 μ; evenly distributed; entirely solitary; oval in shape with the longer axis radial; vessel pitting inconspicuous, small, bordered (vestured), diameter 3-5 μ; perforation plates simple; occasionally occluded with light yellow, lustrous infiltration. *Rays* uniseriate or biseriate; heterogeneous with several rows of upright cells, (disjunctive); vessel-ray pitting small, 6-8 μ; (half-bordered, with narrow border but appearing simple, rounded to elongated); dark-coloured gummy infiltrations abundant; crystals not observed; (silica present in procumbent cells). *Parenchyma* apotracheal, diffuse, tending to link up into short, irregular, wavy lines; some paratracheal, incompletely vasicentric; crystals not observed. *Fibres* moderately thick-walled, non-septate; pits distinctly bordered.

(iii) *Material.*—Herbarium samples of twig material from Java, New Guinea, and northern Australia.

(*w*) *Pilidiostigma*

(i) *General.*—A small genus confined to Australia, species of which were formerly ascribed to *Myrtus* L. One species was available for examination; the heartwood of this is pale brown to red-brown, moderately fine and uniform-textured, of medium density.

(ii) *Structure.*—*Growth rings* not evident. *Vessels* small and indistinct to the naked eye; maximum tangential diameter 130 μ; member length 590 μ; numerous, 15/sq. mm; evenly distributed; entirely solitary; vessel pitting small, bordered, vestured, diameter 4-5 μ; perforation plates simple. *Vasicentric tracheids* present, often merging into fibre tracheids. *Rays* tending to two widths, uniseriate all of upright cells, and multiseriate 3-5-seriate, of procumbent cells with uniseriate margins of 1 to several upright cells; up to 35 cells high; vessel-ray pitting small, half-bordered, and similar to vessel pitting; extraneous material present; no silica or crystals observed. *Parenchyma* moderately abundant, apotracheal, diffuse; no crystals observed. *Fibres* moderately thin-walled, non-septate, with numerous distinctly bordered pits on radial and tangential walls; mean length 1.21 mm.

(iii) *Material.*—*Pilidiostigma* sp. unassigned, one sample north-eastern Australia.

(*x*) *Piliocalyx*

(i) *General.*—A small genus of trees and shrubs confined to New Caledonia; a sample from one species was available for examination; the wood of this sample is light brown; moderately light, medium-textured, with no lustre or figure.

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* Description based mainly on Panshin (1932). In the text the bracketed parts refer to features observed in twig material but not mentioned by Panshin.

(ii) *Structure.—Growth rings* indistinct. *Vessels* small and indistinct to the naked eye; maximum tangential diameter 150 μ; mean member length 760 μ; numerous, 18/sq. mm; solitary, 25 per cent., and in radial multiples up to 5, also a few irregular clusters; perforation plates simple; vessel pitting medium-sized, bordered, alternate, vestured; diameter 8-10 μ; deposits and tyloses absent. *Vasicentric tracheids* absent. *Rays* 1-4-seriate, majority of multiseriates 3 or 4 cells wide; uniseriate composed of square to upright cells; up to 31 cells high, heterogeneous with several rows of square to upright cells at margins; vessel-ray pitting half-bordered, the apertures large and almost coinciding with the borders, rounded to sometimes elongated and occasionally in scalariform arrangement; deposits of extraneous material sparse, mainly in central cells; crystals and silica not observed. *Parenchyma* abundant paratracheal, aliform to confluent in loose, irregular, wavy bands 3-6 cells wide; deposits of extraneous material sparse; crystals aggregated in individual cells of strands. *Fibres* moderately thick-walled, non-septate; pits few, small, and indistinctly bordered; length 1.49 mm.

(iii) *Material.—Piliocalyx latifolium* Brongn. & Gris., one sample New Caledonia.

(*y*) *Pleurocalyptus*

(i) *General.*—A monotypic genus confined to New Caledonia, only herbarium material of which was available for examination.

(ii) *Structure.*—The size of the material (1-year-old twig) was insufficient for a detailed description but features of note were vessel-ray pits half-bordered but apparently simple with large rounded apertures (eucalypt type), and the presence of siliceous inclusions in the central ray cells.

(iii) *Material.—Pleurocalyptus deplanchei* Brongn. & Gris. from Mt. Koghi, New Caledonia.

(*z*) *Rhodamnia*

(i) *General.*—A small genus of medium-sized or small trees with a few species occurring in Malaysia and the Solomon Is., but mainly in New Guinea and Australia. The heartwood is pink to red-brown or sometimes grey-brown in colour, fine and even-textured, moderately heavy, straight-grained or interlocked; six species were available for examination.

(ii) *Structure.—Growth rings* sometimes marked by a narrow to fairly wide band of denser fibres, usually characterized by fewer pores than the remainder of the growth ring. *Vessels* small and indistinct but visible to the naked eye; maximum tangential diameters 88-145 μ; mean member length 470-780 μ; moderately numerous to numerous, 7-24/sq. mm; predominantly to exclusively solitary; somewhat variable in size in the one specimen; vessel pitting small, bordered, vestured, diameter 3-5 μ; perforation plates simple; white deposits common in most species. *Vasicentric tracheids* present. *Rays* 1-8-seriate, mostly of two widths (Plate 7, Fig. 6), uniseriate and 3-6-seriate (sometimes up to 8); uniseriate numerous, composed entirely of upright cells generally less than 15 cells high; multiseriate heterogeneous, composed of procumbent cells in the central portion and uniseriate margins of upright cells, disjunctive; vessel-ray pits small, half-bordered, and similar to vessel type; no silica or crystals observed; deposits of extraneous material abundant throughout rays. *Parenchyma* abundant, apotracheal, diffuse or tending to form short, discontinuous lines, 1 cell wide; also a tendency for aggregations of cells in tangential patches 3-6 cells wide independent of the vessels; paratracheal, incompletely vasicentric, and characteristically in the form of wing-like extensions from the abaxial side of the pores; crystals absent, except in *R. cinerea* where they are numerous, large, and elongated, occurring singly and occupying most of the cell cavity (Plate 9, Fig. 5); deposits of extraneous material abundant. *Fibres* thick-walled, non-septate; with numerous distinctly bordered pits; mean length 1.20-1.40 mm.

(iii) *Material.—Rhodamnia acuminata* C. T. White, one sample north-eastern Australia; *R. argentea* Benth., five samples north-eastern Australia; *R. blairiana* F. Muell., one sample New Guinea; *R. cinerea* Jack., one sample New Guinea; *R. sessiliflora* Benth., two samples north-eastern Australia; *R. trinervia* Bl., seven samples north-eastern Australia.

(*aa*) *Rhodomyrtus*

(i) *General.*—A genus of a few species of medium-sized to small trees occurring mainly in New Guinea, New Caledonia, and Australia. The heartwood is pale pink to grey-brown, moderately heavy, fine and uniform-textured.

(ii) *Structure.—Growth rings* indistinct. *Vessels* small and indistinct to the naked eye; maximum tangential diameter 98-127 μ; mean member length 630-880 μ; evenly distributed; numerous, 11-15/sq. mm; uneven in size; entirely to 90 per cent. solitary; perforation plates simple; vessel pitting small, bordered, vestured, diameter 4-5 μ; no tyloses or deposits observed. *Vasicentric tracheids* present. *Rays* 1-3-seriate, occasionally up to 4, markedly heterogeneous, multiseriate with 1 to several rows of upright cells, uniseriate composed of upright cells only, numerous; multiseriate up to 30 cells high; vessel-ray pitting small, half-bordered, and similar to vessel type, though smaller; silica and crystals absent; deposits of extraneous material abundant. *Parenchyma* abundant apotracheal, diffuse, tending in *R. macrocarpa* to link up into loose tangential bands; also sparse paratracheal; deposits of extraneous material present; crystals in individual cells of strands present in *R. macrocarpa*. *Fibres* moderately thin to thick-walled, non-septate with small, but distinctly bordered pits; mean length 1.20-1.60 mm.

(iii) *Material.—Rhodomyrtus macrocarpa* Benth., two samples north-eastern Australia; *R. psidioides* (G.Don) Benth., one sample north-eastern Australia; *R. timonioides* L. S. Smith mspt., one sample New Guinea; *Rhodomyrtus* sp. (*Myrtus beckleri* F. Muell.), one sample north-eastern Australia.

(*bb*) *Spermolepis*

(i) *General.*—A monotypic genus confined to New Caledonia; the botanical position of this genus in the family is doubtful; anatomically it is allied to *Angophora* and *Eucalyptus*; it is a quite important timber tree in New Caledonia and is exported with other species to Australia. The heartwood is pink to red-brown, dense, medium-textured, grain generally wavy and interlocked; gum veins present.

(ii) *Structure.—Growth rings* not distinct. *Vessels* visible to the naked eye but not distinct owing to the presence of tyloses; maximum tangential diameter 214 μ; mean member length 660 μ; moderately numerous, 5/sq. mm, tending to be distributed in tangential zones with intermediate areas more or less free of vessels; entirely solitary but with some slight oblique tendency; vessel pitting moderately coarse, bordered, vestured, diameter 7-12 μ; perforation plates simple; tyloses abundant. *Vasicentric tracheids* present. *Rays* mainly uni- or biseriate, sometimes triseriate in part; maximum height up to 18 cells; weakly heterogeneous with several rows of cells greater in vertical dimensions than the central procumbent, to squarish and occasionally vertically elongated; vessel-ray pitting large, half-bordered, with narrow border, and appearing simple, round to oval or elongated, and resembling those of *Eucalyptus* and *Angophora* (Plate 8, Fig. 5); deposits of extraneous material moderately abundant; crystals and siliceous inclusions absent. *Parenchyma* apotracheal, diffuse, sparse to moderately abundant, tending to link up into loose tangential bands (Plate 5, Fig. 6); crystals absent; deposits of extraneous material infrequent. *Fibres* thick-walled, non-septate, with distinctly bordered pits; length 1.30 mm.

(iii) *Material.—Spermolepis gummifera* Brongn. & Gris., three samples New Caledonia; twig material from genotype.

(*cc*) *Syncarpia*

(i) *General.*—A small genus confined to eastern Australia; S. *hillii* has a restricted distribution on Fraser I. and the mainland immediately adjacent; both it and S. *procera* are large trees of commercial importance. The heartwood is pale pinkish brown to dark red, moderately heavy to heavy, uniform and fine-textured, sometimes straight-grained but also interlocked and wavy. S. *procera* is used mainly for marine piling, wharf decking, and general heavy construction, posts, sleepers, and house construction as stumps, plates, sills, and joists. S. *hillii* is slightly less dense than S. *procera* and is used for furniture, interior fittings, and flooring.

(ii) *Structure.—Growth rings* usually not marked. *Vessels* small and indistinct to the naked eye; maximum tangential diameter 145 μ; mean member length 650-810 μ; evenly distributed; numerous, 11-22/sq. mm; entirely solitary; vessel pitting small, bordered, vestured, diameter 5-7 μ; perforation plates simple; tyloses present but not abundant; white or yellowish deposits present in both species, these appear under the microscope to be associated with small granular crystalline deposits. *Vasicentric tracheids* present. *Rays* uni- or biseriate, weakly heterogeneous with 1 to several rows of squarish cells, height up to 30 cells, chiefly below 25; vessel-ray pits small, half-bordered with narrow border and appearing simple, round to elongated; siliceous inclusions abundant, imbedded in clear gum, confined mainly to the central procumbent cells; crystals not observed; deposits of extraneous material abundant. *Parenchyma* sparse to moderately abundant, diffuse, some paratracheal, incompletely vasicentric, chiefly located on abaxial side of the pores; deposits of extraneous material present; no siliceous inclusions observed, fine crystalline deposits resembling those in the vessels also present in many cells. *Fibres* moderately thin to thick-walled, non-septate, with distinctly bordered pits; mean length 1.14-1.34 mm.

(iii) *Material.—Syncarpia hillii* F. M. Bail., 10 samples eastern Australia; *S. procera* (Salisb.) Domin, 25 samples eastern Australia.

(*dd*) *Tristania*

(i) *General.*—A genus of some 20 species of moderate-sized to large trees occurring from south-east Asia and Malaysia, to Australia, New Caledonia, and Fiji. The majority of the species from Malaya, Borneo, and the Philippines are small trees though their timbers are described as being dense, strong, and durable and of some local use for piling, bridge and wharf decking, etc. (Burkill 1935). The heartwood is pinkish to red-brown or dark brown, moderately heavy to heavy, fine and uniform-textured with occasionally straight but generally wavy or interlocked grain; three of the species examined, including *T. conferta* and *T. suaveolens,* show the presence of a waxy substance in the wood when shavings are boiled in water. The Australian species *T. conferta* has a wide range of uses, chiefly in the heavy construction field, but is also used for house construction, framing, and flooring.

(ii) *Structure.—Growth rings* seldom visible. *Vessels* varying from small and invisible to the naked eye to intermediate and distinct to the naked eye; maximum tangential diameters 72-200 μ in different species; mean member length 480-860 μ; moderately numerous to very numerous, 7 to more than 20/sq. mm; almost entirely to exclusively solitary, variable in size; generally evenly distributed, sometimes with a tendency to zonation with few pores in the late wood, occasionally with a marked oblique tendency in localized areas; vessel pitting small, bordered, vestured, diameter 5-7 μ; perforation plates simple; tyloses generally present, sometimes abundant; white and orange to red-brown deposits present. *Vasicentric tracheids* present. *Rays* uniseriate to partly biseriate; less than 20 cells high; weakly heterogeneous with few cells squarish or of greater vertical dimensions than the central procumbent; in 3 species 1 to several rows of upright cells grading to square or brick-shaped in the centre, true procumbent cells lacking; vessel-ray pits small, half-bordered, with narrow border, and appearing simple, rounded to sometimes irregular or elongated; siliceous inclusions present in all species, mainly located in the central procumbent cells (Plate 7, Fig. 3), but also in the marginal cells in the specimen from the Philippines; deposits of extraneous material abundant; no crystals observed. *Parenchyma* apotracheal, diffuse, sparse to moderately abundant, with a tendency to form short, uniseriate lines or infrequent discontinuous bands; paratracheal sparse, but in 2 species abaxial extending into short tangential wings; crystals absent; deposits of extraneous material abundant. *Fibres* moderately thick to very thick-walled, non-septate with small, distinctly bordered pits; mean length 0.96-1.28 mm.

(iii) *Material.—Tristania conferta* R. Br., 30 samples eastern Australia; *T. exiliflora* F. Muell., two samples north-eastern Australia; *T. grandiflora* Cheel., three samples northern Australia; *T. laurina* R. Br., 16 samples eastern Australia; *T. lactiflua* F. Muell., three samples north-eastern Australia; *T. merguensis* Griff., one sample Malaya; *T. neriifolia* R. Br., one sample eastern Australia; *T. obovata* R. Br., one sample North Borneo; *T. suaveolens* Sm., 14 samples eastern Australia; *T. suaveolens* Sm. var. *glabrescens* Bail., one sample north-eastern Australia; *T. pachysperma* (F. Muell. & F. M. Bail.) Francis (= *Xanthostemon pachyspermus* F. Muell. & F. M. Bail.), three samples north-eastern Australia; *Tristania* sp. unassigned, one sample Philippines.

(*ee*) *Xanthomyrtus*

(i) *General.*—A genus consisting of some 22 species of trees centred mainly in New Guinea (19), extending to New Caledonia (2), Borneo (3), the Philippines (1), and Australia (1); the two species available for examination were from only moderate-sized trees 50-90 ft high. The heartwood is red-brown or brown to deep brown, heavy, fine and uniform-textured, straight-grained or slightly interlocked.

(ii) *Structure.—Growth rings* inconspicuous. *Vessels* small and indistinct to the naked eye; maximum tangential diameter 102-122 μ; mean member length 850-960 μ; evenly distributed and numerous, 15-22/sq. mm; up to 55 per cent. solitary, the remainder in radial multiples of 2-3, occasionally up to 4; vessel pitting fine, bordered, alternate, loosely arranged, vestured, diameter 5-6 μ; perforation plates simple; white deposits present in both species. *Vasicentric tracheids* present, few. *Rays* tending to be of two widths, uniseriate composed entirely of upright cells, up to 10 cells high, and multiseriate 3-5 cells wide in procumbent portion with uniseriate margins of 1 to several rows of upright cells, disjunctive, up to 35 cells high; vessel-ray pitting small, half-bordered, the apertures almost coinciding with the border and appearing simple and rounded; deposits of extraneous material abundant; no crystals or siliceous inclusions present. *Parenchyma* moderately abundant; apotracheal, diffuse, in short lines between vessels, some paratracheal; deposits of extraneous material sparse to abundant; no crystals or siliceous inclusions present. *Fibres* extremely thick-walled with very small lumen, pits moderately numerous, simple to indistinctly bordered, length 1.53-1.69 mm.

(iii) *Material.—Xanthomyrtus longicuspis* Diels, one sample New Guinea; *Xanthomyrtus* sp. unassigned, one sample New Guinea.

(*ff*) *Xanthostemon*

(i) *General.*—A genus closely allied to *Metrosideros* with its centre of distribution in New Caledonia, with 33 endemic species, but extending to northern and north-eastern Australia (5), New Guinea (4), Philippines (4), and Celebes (1) (Merrill 1952). Samples from seven species were available for examination. The heartwood of these timbers varies from dark brown to red-brown or sometimes yellowish brown; heavy in all species but *X. chrysanthus,* which is only moderately heavy; fine and uniform-textured, often interlocked in the grain; most species are reported to be durable and several are used commercially for posts, stumps, and piling, particularly marine piling, and for heavy construction generally.

(ii) *Structure.—Growth rings* ill-defined. *Vessels* small and barely visible to the naked eye; maximum tangential diameters 85-178 μ; mean member length 670-820 μ; numerous to very numerous (9-20 +/sq. mm); evenly distributed and entirely solitary; vessel pitting small, bordered, vestured, diameter 4-7 μ; perforation plates simple; tyloses abundant and sometimes sclerosed, gummy inclusions also abundant; white deposits present. *Vasicentric tracheids* present. *Rays* uniseriate to sometimes biseriate; generally less than 20 cells high; practically homogeneous to weakly heterogeneous with 1 or 2 rows of squarish to upright cells; vessel-ray pits small, half-bordered but appearing simple, rounded to irregular, and varying in size between species; deposits of extraneous material abundant, siliceous inclusions abundant in all species, mainly or exclusively confined to central cells of the ray. *Parenchyma* apotracheal, diffuse, sometimes tending to link up into short, irregular, tangential lines; deposits of extraneous material abundant. *Fibres* thick-walled, non-septate, pits distinctly bordered; length 1.00-1.35 mm.

(iii) *Material.—Xanthostemon brachyandrus* C. T. White, one sample north-eastern Australia; *X. chrysanthus* F. Muell., two samples north-eastern Australia; *X. kassikassi* L. S. Smith, four samples New Guinea; *X. oppositifolius* F. M. Bail., one sample north-eastern Australia; *X. paradoxus* F. Muell., one sample north-eastern Australia; *X. verdugonianus* Naves, one sample Philippines; *X. whitei* Gugerli (= *X. pubescens* C. T. White), one sample north-eastern Australia.

III. SUMMARY OF ANATOMICAL FEATURES OF THE FAMILY

(*a*) *Based on the Examination of* 32 *Genera occurring in the South-west Pacific Area*

(i) *Growth Rings.*—Generally poorly defined but occasionally indicated by bands of denser late wood fibres as in *Eucalyptus gigantea* (Plate 6, Fig. 6), no genera are ring-porous, though in *Leptospermum and Melaleuca* there is a tendency for the pores to be more numerous and somewhat larger toward the early part of the growth ring.

(ii) *Vessels* are characteristically solitary in the majority of genera; radial multiples, usually 2-3, are present and often predominate in *Eugenia B* (including *Acmena, Cleistocalyx,* and *Syzygium*), *Piliocalyx, Angophora, Eucalyptopsis,* and *Xanthomyrtus;* multiples also occur in the bloodwood group of *Eucalyptus.* Distribution of the vessels is generally uniform throughout the family though an oblique alignment of the pores is evident to a greater or less extent in a few genera, notably *Eucalyptus.* Maximum tangential diameter of vessels varies greatly between genera, and within a genus, from 45 μ in some species of *Melaleuca* to 260 μ in some of *Eucalyptus*; vessel members short to moderately long, varying from extremes of 260 to 1,090 μ, the majority falling between 400 and 800 μ; in *Eugenia B* (including *Acmena, Cleistocalyx,* and *Syzygium*) the vessel members vary from 650 to 1,090 μ in length. The vessel members are generally truncate with short to long tails; perforation plates are exclusively simple; vessel pitting is uniformly vestured throughout the family, the diameter of vessel pits varies from 7 to 14 μ in *Eucalyptus, Angophora, Spermolepis, Eugenia B* (including *Acmena, Cleistocalyx,* and *Syzygium*), *Eucalyptopsis,* and *Kjellbergiodendron,* and from 3 to 8 μ in the remainder.

(iii) *Vasicentric tracheids* occur throughout the family with the exception of *Eugenia B* (including *Acmena, Cleistocalyx,* and *Syzygium*), *Eucalyptopsis,* and *Piliocalyx.*

(iv) *Rays.*—In general the rays tend to fall into two types; the first, characteristic of most genera of the Leptospermoideae, are 1-4-seriate, more commonly 1-3, maximum height usually under 25 cells; weakly heterogeneous with few cells at the margins of greater vertical dimensions than the central procumbent, but generally horizontally elongated to squarish with few to no upright cells. The second type is characteristic of the Myrtoideae and these are distinctly heterogeneous in form (Plate 9, Fig. 1); moreover, several of the genera in this group with wider rays show a distinct tendency to a segregation into two widths, typical examples being found in *Eugenia B* (Plate 9, Fig. 2), *Rhodamnia,* and *Decaspermum.* In these the multiseriate rays are 3-4, sometimes up to 6 cells wide, and occasionally (*Rhodamnia*) up to 8 cells wide, and 30-50 cells high with uniseriate margins of upright cells, the uniseriate rays generally up to 10 cells high, and consisting only of upright cells. The remainder of the genera in this group have narrower rays, usually 2-4-seriate, heterogeneous with 1 to several rows of upright cells, but with no tendency for a segregation into two widths, though the uniseriate rays are generally lower and usually composed of upright cells. The vessel-ray pitting varies in form and for the purpose of this examination has been arbitrarily split up into four types (Plate 8):

(1) Small, half-bordered, and similar to vessel type, the diameter of the borders up to 8 μ (Fig. 1);

(2) Small, half-bordered, but with wide aperture and narrow border and appearing simple, rounded to irregular in shape; when regular, the borders up to 8 μ in diameter (Fig. 2);

(3) Moderately large, half-bordered, but with large aperture and narrow border appearing simple; irregular in shape to elongated and often scalariform in arrangement; sometimes unilaterally compound (Fig. 3);

(4) Large, apparently simple, rounded to oval, apertures usually 10-14 μ (eucalyptian) (Figs. 4, 5, and 6).

Type 3 is characteristic of *Eugenia B* (including *Acmena, Cleistocalyx,* and *Syzygium*) and *Piliocalyx* of the *Eugeniinae,* and *Kjellbergiodendron*; type 4 is confined to *Eucalyptopsis, Eucalyptus, Angophora,* and *Spermolepis*; the other two types occur in the remainder of the genera of both Myrtoideae and Leptospermoideae; it is interesting that genera with silica inclusions in the rays all have the same type of vessel-ray pits (type 2). The American genera examined all have vessel-ray pits of type 1, with the exception of *Tepualia*, a genus occurring in Chile, and having close botanical and wood anatomical affinities with *Metrosideros*, a typical Pacific genus. Deposits of extraneous material are abundant in some species of all genera; crystals are characteristically absent; siliceous inclusions have been found in the rays of 10 genera of the Leptospermoideae, *Callistemon, Calothamnus, Lysicarpus, Melaleuca, Metrosideros, Osbornia, Pleurocalyptus, Xanthostemon, Tristania,* and *Syncarpia.* These inclusions are usually present in the central cells of the ray.

(v) *Parenchyma* is chiefly apotracheal in the majority of genera; in some, notably *Agonis, Angophora, Eucalyptopsis, Eucalyptus,* and *Spermolepis,* both apotracheal and paratracheal parenchyma are present in the same wood; in *Eugenia B* (including *Acmena, Cleistocalyx,* and *Syzygium*), *Kjellbergiodendron,* and *Piliocalyx* the parenchyma type is predominantly paratracheal but varying in amount from incompletely vasicentric to weakly confluent, to abundantly vasicentric and confluent, sometimes forming numerous regular bands up to 6 cells wide. In genera with apotracheal parenchyma, this is generally diffusely arranged but with some tendency to link up into short, irregular, and discontinuous lines and occasionally in irregular patches up to several cells wide; where the apotracheal diffuse parenchyma is abundant there is frequently a tendency for a grouping contiguous to the vessels and appearing paratracheal, but confined to the abaxial side and sometimes forming winglike extensions, e.g. *Rhodamnia* and *Tristania* (Plate 7, Fig. 5). Crystal strands (Plate 9, Fig. 4) are numerous in some species of *Angophora, Backhousia, Eucalyptus, Eugenia A, Eugenia B* (including *Acmena, Cleistocalyx,* and *Syzygium*), *Piliocalyx,* and *Kjellbergiodendron*; large crystals in enlarged parenchyma cells, sometimes solitary, but more often in vertical series of 2 to several, were observed in some species of *Agonis, Eugenia A, Kunzea,* and *Leptospermum* and large, elongated crystals (Plate 9, Fig. 6) were observed in a species of *Rhodamnia.* Deposits of extraneous material are variable from absent to abundant.

(vi) *Fibres* are moderately thin to thick-walled, non-septate; with distinctly bordered pits in all genera except *Eugenia B* (including *Acmena, Cleistocalyx,* and *Syzygium*), *Piliocalyx, Eucalyptopsis,* and *Xanthomyrtus,* in which only simple to indistinctly bordered pits are present. Average length of those of the the former group varies from 0.43 to 1.53 mm, of the latter from 1.10 to 1.90 mm.

(vii) *Vertical concentric canals* of the lysigenous type (Plate 6, Fig. 5) are a common feature of the woods of three genera, *Angophora, Eucalyptus,* and *Spermolepis.* These develop into large lens-shaped concentric pockets or gum-veins extending for considerable vertical distances in the wood.

(*b*) *Anatomy of American Genera*

There are approximately 20 arborescent genera and several hundred species of the Myrtaceae occurring in America which have been described anatomically by Record and Hess (1943), all of which, with one exception, belong to the Myrtoideae; the exception, *Tepualia,* is monotypic and is related botanically and wood anatomically to *Metrosideros* of the Leptospermoideae. This genus has a wide distribution in the Pacific from Hawaii to New Zealand, New Guinea, and northern Australia, with one species reported from Africa. Samples from 13 genera were examined and their anatomy compared with that of the south-west Pacific genera.

These genera, except *Tepualia,* reveal an essential similarity in the following features:

(i) Vessel-ray pitting exclusively small, half-bordered, and similar to the vessel type.

(ii) Heterogeneous rays with a tendency for the marginal upright cells to be disjunctive.

(iii) Parenchyma essentially apotracheal, diffuse but tending to short, discontinuous lines or bands.

(iv) Vessels, with the exception of three genera, predominantly to exclusively solitary. All genera examined have vestured pits and exclusively simple perforation plates.

The genus *Tepualia* differs from the above in having vessel-ray pits which, although half-bordered, appear simple and rounded to elongated. Several genera have solitary large crystals in the vertical parenchyma, sometimes singly, but more often in vertical series (this is also shown by two species of *Leptospermum,* one species of *Agonis,* and one species of *Kunzea*).

Three specimens of *Jambosa vulgaris* DC. were received from Venezuela through the courtesy of Professor Hess, Yale School of Forestry. This species is of East Indian origin and may have escaped from cultivation. Anatomically the wood agrees with the group *Eugenia B* but is characterized by the presence of siliceous inclusions in the vertical parenchyma. Such inclusions have not been observed in *Eugenia B* of south-west Pacific origin, nor in vertical parenchyma of any other genus.

(*c*) *General*

The examination of the wood anatomy of the Myrtaceae does not reveal many consistent, clear-cut anatomical features common to all genera, as is the case in some other families. There are a few such characteristic features, but on the other hand a number of divergences are apparent which are to some extent consistent with botanical classifications within the family. The summary of anatomical features for the family can best be listed as follows:

(i) *Features Common to All Genera*

(1) Pitting of vessels and tracheary elements exclusively vestured;
(2) Perforation plates simple;
(3) Rays never truly homogeneous;
(4) Absence of calcium oxalate crystals from the ray cells.

(ii) *Features Common to Nearly All Genera*

(1) Vasicentric tracheids—except in *Eugenia B, Piliocalyx,* and *Eucalyptopsis;*
(2) Fibres with conspicuously bordered pits (fibre tracheids)—except in *Eucalyptopsis, Eugenia B, Piliocalyx,* and *Xanthomyrtus;*

(3) Predominantly to exclusively solitary vessels—except in *Xanthomyrtus*, *Eugenia B*, *Eucalyptus B* (bloodwood group), *Piliocalyx*, *Eucalyptopsis*, and *Angophora*.

(iii) *Features in which Considerable Divergences Exist*

(1) Rays—of two distinct widths or distinctly heterogeneous, or both, in the Myrtoideae; weakly heterogeneous and of one type in the Leptospermoideae (with one or two exceptions);
(2) Ray-vessel pits—four types as listed above;
(3) Parenchyma—exclusively apotracheal, mainly diffuse in majority of genera; paratracheal and apotracheal in some; predominantly paratracheal to confluent in narrow to wide bands in *Eugenia B* and *Piliocalyx*;
(4) Siliceous inclusions—in 10 genera of the Leptospermoideae, chiefly in the central cells of the rays.

A grouping of the various genera of the family occurring in the south-west Pacific area, based on anatomical features, has been set out in Table 3.

IV. Discussion

In a review of the Myrtaceae it is difficult to point to any one anatomical feature which separates the Myrtoideae from the Leptospermoideae, but the type of ray encountered in the two groups does form some basis for distinction, with one or two exceptions. This question of ray type and function is a very vexed one, involving definitions of terms and the relation of form to function. In this report the definitions of the International Association of Wood Anatomists relating to form rather than to function have been followed. Truly homogeneous rays are lacking in the family but certain distinctions can be observed, namely (*a*) definitely heterogeneous multiseriate rays with few to many rows of upright cells, the uniseriate rays usually composed only of upright cells, and (*b*) weakly heterogeneous rays with marginal cells of square or brick-like form but seldom greater in vertical dimensions than horizontal, and uniseriate rays similar to the multiseriate. Table 4 shows the division of the genera of the south-west Pacific area on this basis. It will be noted that they fall into the two main subfamilies with the exception of some species in a few of the genera of the Leptospermoideae. Most of the genera of the Leptospermoideae possess weakly heterogeneous rays with no tendency for segregation into two widths as is frequently shown by genera of the Myrtoideae. The characteristic ray type of the Leptospermoideae is found in *Eucalyptus* or *Backhousia*, generally 1-3 cells wide and under 20 cells high (Plate 9, Fig. 3), often heterogeneous in function as instanced by the segregation of inclusions (e.g. silica in other genera of the subfamily), but with a virtual absence of upright cells sharply separated from the central procumbent cells. On the other hand the rays of the Myrtoideae, in several genera, are of two distinct widths, the low uniseriate rays composed entirely of upright cells, and the multiseriate with margins of one to several rows and a central portion of procumbent cells. The rays of the

TABLE 3

GROUPING OF 32 OF THE GENERA OCCURRING IN THE SOUTH-WEST PACIFIC AREA, BASED ON ANATOMICAL FEATURES

I. Vasicentric tracheids present, fibres with conspicuously bordered pits on radial and tangential walls	
A. Vessel-ray pits large, simple rounded to oval; parenchyma both paratracheal and apotracheal in the same wood; siliceous inclusions absent; rays homogeneous to weakly heterogeneous	
1. Vessels entirely solitary	
a. Apotracheal parenchyma diffuse, seldom banded	*Eucalyptus A*
b. Apotracheal parenchyma generally in fine lines or banded	*Spermolepis*
2. Vessels in radial multiples	*Eucalyptus B, Angophora*
B. Vessel-ray pits small and similar to vessel type; parenchyma predominantly apotracheal; siliceous inclusions absent	
1. Rays weakly heterogeneous	
a. Vessels predominantly to exclusively solitary	*Backhousia, Choricarpia, Leptospermum* p.p., *Kunzea, Baeckia*
b. Up to 25 per cent. of vessels in radial multiples	*Leptospermum* p.p., *Agonis*
2. Rays distinctly heterogeneous with more than 3 rows of upright cells	*Decaspermum, Eugenia A, Austromyrtus, Octamyrtus, Pilidiostigma, Rhodamnia, Rhodomyrtus*
C. Vessel-ray pits small to medium-sized, apparently simple, round to sometimes elongated; parenchyma predominantly apotracheal	
1. Siliceous inclusions present	
a. Rays weakly heterogeneous; siliceous inclusions chiefly in central ray cells	*Callistemon, Calothamnus, Lysicarpus, Melaleuca*, Osbornia, Syncarpia, Tristania, Xanthostemon*
b. Rays heterogeneous with more than 3 rows of upright cells; siliceous inclusions abundant in 1 species, sparse or sporadic in others	*Metrosideros*
2. Siliceous inclusions absent	*Lophomyrtus*
D. Vessel-ray pits moderately large, elongated to scalariform	*Kjellbergiodendron*
II. Vasicentric tracheids present, fibres with simple to indistinctly bordered pits; more than 50 per cent. of vessels in radial multiples	*Xanthomyrtus*

TABLE 3 (*Continued*)

III. Vasicentric tracheids absent, fibres with simple to indistinctly bordered pits	
A. Parenchyma both paratracheal, aliform to confluent, and apotracheal diffuse; vessel-ray pits large, simple, round to oval; rays weakly heterogeneous, uni- or biseriate	*Eucalyptopsis*
B. Parenchyma essentially paratracheal, aliform to confluent, often banded; vessel-ray pits moderately large, elongated to scalariform and sometimes unilaterally compound; rays distinctly heterogeneous, often of two widths, uniseriate of upright cells, and multiseriate 3-5	*Eugenia B* (*Acmena, Cleistocalyx, Syzygium*) *Piliocalyx*

* *Melaleuca leucadendron* has vessel-ray pitting nearly as coarse as the eucalypt type (Plate 8, Fig. 7) but differs from *Eucalyptus, Angophora,* and *Spermolepis* in parenchyma arrangement and the presence of siliceous inclusions in the rays; and from *Eucalyptopsis* in the presence of vasicentric tracheids and distinctly bordered pits between fibres.

remainder of the genera of the Myrtoideae are distinctly heterogeneous in form but not of two distinct widths. In the Leptospermoideae the genera *Kunzea, Leptospermum, Melaleuca, Metrosideros, Osbornia,* and *Xanthostemon* have some species with rays approaching the heterogeneous type. It should be noted that siliceous inclusions in the ray cells are found only in genera belonging to the Leptospermoideae.

A critical examination of the anatomy of the family reveals several interesting facts. Perhaps the most striking is the divergence from a generally similar pattern of the group termed for convenience *Eugenia B*. This group includes *Acmena, Cleistocalyx, Syzygium,* and a number of species still referred to *Eugenia,* all occurring in south-eastern Asia, Malaysia, and the south-west Pacific.

Anatomically the group is characterized by paratracheal to confluent parenchyma, vessels often predominantly in radial multiples, fibres with simple to indistinctly bordered pits (libriform), absence of vasicentric tracheids, and distinctive elongated to gash-like vessel-ray pits. In all these features it is quite distinct from *Eugenia A,* covering mainly the New World species. These points of difference are anatomically fundamental and clearly indicate that more than one genus is covered by *Eugenia* (sens. lat.). In an earlier publication the authors (Dadswell and Ingle 1947) pointed out that Merrill and Perry were justified on anatomical grounds in separating the Old World species from the remainder. Henderson (1949) has retained *Eugenia* (sens. lat.) but proposed several sections within the genus, namely §*Eu-eugenia* (= *Eugenia* sens. str.), §*Cleistocalyx,* §*Syzygium,* §*Acmena,* and §*Fissicalyx.* His point is that it is difficult to find a satisfactory basis for splitting *Eugenia* on seed characters, although better characters might be found in the structure of the inflorescence and flowers. It is suggested that the anatomy of the wood provides ample characters for making a split, and it is logical to do so even though the splitting of such a well-known genus would bring objections from "foresters, agriculturalists, horticulturalists and others who are perfectly familiar with the name *Eugenia*" (Henderson 1949). This suggested split on anatomical grounds involved only the two groups *Eugenia A* and *Eugenia B*; there is no anatomical support for the separation of *Acmena, Cleistocalyx*, or *Syzygium*. In a recent publication Merrill (1950*b*) decided to follow Diels in recognizing *Jossinia* Commers. as a valid genus covering the few species of *Eugenia* (sens. str.) occurring in Africa, Madagascar, Malaysia, and Polynesia. This is logical since *Eugenia* would then be restricted, without exception, to the tropics of the New World. However, this is in the botanical field, as wood anatomically the New World species of *Eugenia A* are indistinguishable from those of the Old World tropics whether they be *Eugenia* L. or *Jossinia* Commers.

TABLE 4

COMPARISON OF RAY TYPE BETWEEN THE GENERA OF THE MYRTOIDEAE AND THE LEPTOSPERMOIDEAE OCCURRING IN THE SOUTH-WEST PACIFIC AREA

Myrtoideae Genus	Predominant Width (No. of cells)	Distinctly Heterogeneous, Uniseriate All of Upright Cells	Leptospermoideae Genus	Predominant Width (No. of cells)	Weakly Heterogeneous, Uniseriate Similar to Multiseriate
Austromyrtus	1 (2) 3-4	+	*Agonis*	1-4	+
Decaspermum	1, 3-4	+	*Angophora*	1-2	+
Eugenia A	1, 2-3	+	*Backhousia*	1-2(3)	+
Eugenia B			*Baeckia*	1-2	+
Acmena	1, 3-5	+	*Callistemon*	1-3	+
Cleistocalyx	1, 2-3(4)	+	*Calothamnus*	1-(2)	+
Syzygium	1 (2) 3-5	+	*Choricarpia*	1-2	+
Lophomyrtus	1, 2-(3)	+	*Eucalyptopsis*	1-(2)	+
Octamyrtus	1, 2-3	+	*Eucalyptus*	1-3 (4)	+
Pilidiostigma	1, 3-5	+	*Kunzea*	1-3	∓
Piliocalyx	1, 3-4	+	*Leptospermum*	1-3(4)	∓
Rhodamnia	1, 3-6 (8)	+	*Lysicarpus*	1-(2)	+
Rhodomyrtus	1, 3-(4)	+	*Melaleuca*	1-2 (3)	±
Xanthomyrtus	1, 3-5	+	*Metrosideros*	1-2 (3)	+
			Osbornia	(1-2)	(—)
			Spermolepis	1-2	+
			Syncarpia	1-2	+
			Tristania	1-2	+
			Xanthostemon	1-3	±
Kjellbergiodendron 1-2 (Sometimes heterogeneous; uniseriate similar to multiseriate)					

∓ Minority of species conforming; ± majority of species conforming; (—) not observed.

The anatomy of the New Caledonian genus *Piliocalyx* is similar to *Eugenia B* and this agrees with the placing of the genus in Niedenzu's botanical classification. *Myrciaria*, the only other genus of the Eugeniinae from the New World available for examination, is anatomically similar to *Eugenia A*.

The group *Eucalyptus, Angophora,* and *Spermolepis* is distinctive in that all species show the large, rounded type of vessel-ray pit (eucalypt type), both paratracheal and apotracheal parenchyma, a strong tendency for oblique arrangement of vessels and vessel multiples, and gum veins of the lysigenous type. *Spermolepis* seems to form a link between *Eucalyptus* and *Angophora* In its strong development of paratracheal, confluent parenchyma it resembles *Angophora* and *Eucalyptus B* ("bloodwood" group), but resembles *Eucalyptus A* in its exclusively solitary vessels. In the Niedenzu classification *Spermolepis* is, however, placed in the Metrosiderinae close to *Metrosideros,* whereas anatomically it is closely allied to the Eucalyptinae.

The new genus *Eucalyptopsis* has some affinity anatomically with the group *Eucalyptus, Angophora,* and *Spermolepis* in its ray type and vessel-ray pitting; on the other hand the absence of fibres with distinctly bordered pits and of vasicentric tracheids would indicate a relationship with the *Eugenia B* section of the Eugeniinae. White (1951) has said that *Eucalyptopsis* is most closely allied to *Pleurocalyptus* botanically and is akin to *Syncarpia* and *Choricarpia,* all of which have been placed by Niedenzu in the Metrosiderinae.

The late Mr. C. T. White, in a personal communication, said that *Pleurocalyptus* is akin to *Eucalyptus* and *Angophora*; unfortunately only twig material of this genus was available for examination but the vessel-ray pits are certainly similar to the eucalypt type. However, the rays show abundant deposits of silica in the central cells, a feature not found in the Eucalyptinae but observed in four genera of the Metrosiderinae.

Domin (1928) made the genus *Choricarpia* to cover *Syncarpia leptopetala* F. Muell. In this paper *Choricarpia* has been accepted as a separate genus and under it both *Syncarpia leptopetala* and *Syncarpia subargentea* C. T. White have been considered. These two species differ anatomically from *Syncarpia procera* (Salisb.) Domin and *Syncarpia hillii* F. M. Bail. as follows:

	Choricarpia	*Syncarpia*
Vessel-ray pits	Similar to inter-vessel type	Small, appearing simple, rounded
Siliceous inclusions	Absent	Abundant in ray cells
Parenchyma	Apotracheal, tendency to narrow bands	Paratracheal sparse and apotracheal diffuse

The diversity of parenchyma distribution in this family should be noted; practically all types of apotracheal and paratracheal are represented, and frequently both in the one wood. In describing the paratracheal parenchyma it has frequently been found hard to give an accurate estimate of its extent because of the difficulty of dissociating it, in some genera, from vasicentric tracheids in cross section, and in others from fibre tracheids. No such difficulty is encountered in the *Eugenia B* group of the Eugeniinae (with paratracheal to confluent parenchyma) since no vasicentric tracheids or fibre tracheids are present.

In many genera with both apotracheal and paratracheal parenchyma, notably *Austromyrtus, Backhousia, Eucalyptus A, Rhodamnia, Syncarpia,* and *Tristania,* there is present a type of parenchyma which has been referred to as

TABLE 5

SPECIES DISTRIBUTION OF GENERA OCCURRING IN THE SOUTH-WEST PACIFIC AREA COVERED BY THIS WORK

	Agonis	*Angophora*	*Austromyrtus*	*Backhousia*	*Baeckia*	*Callistemon*	*Calothamnus*	*Choricarpia*	*Decaspermum*	*Eucalyptopsis*	*Eucalyptus*	*Eugenia A*	*Eugenia B**	*Kjellbergiodendron*	*Kunzea*	*Leptospermum*	*Lophomyrtus*	*Lysicarpus*	*Melaleuca*	*Metrosideros*	*Octamyrtus*	*Osbornia*	*Pilidiostigma*	*Piliocalyx*	*Pleurocalyptus*	*Rhodamnia*	*Rhodomyrtus*	*Spermolepis*	*Syncarpia*	*Tristania*	*Xanthomyrtus*	*Xanthostemon*
India									1			+ ?	79																	1		
Burma													+ ?																	4		
Malaya									1				139			1			1	1						1	1			3		
Indo-China, Siam ..					+ ?								105													1						
Sumatra, Java									2				55			2				+ ?						1				1		
Borneo													168														+ ?			5	3	
Celebes, Moluccas ..									1	1		+ ?	+ ?	3							1 ?					1						1
Philippines									6		1	9†	200							1		1					2			5	1	4
New Guinea					1				10	2	5	3†	159			2			2	7 ?	5	1				6	2			3	19	4
Australia	13	7	13	7	60	12	25	2	1		600 +	2	21		20	30		1	100 +	2		1	4			5	6		2	9		5
New Caledonia ..			12 +		5				1			4 ?	52 ?						2	11				4	1		5	1		5	2	33
Solomon Is.												1	15							1						1						
New Zealand													1			2	3			8												
Samoa													20							1												
Fiji									1				5							1										1		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32

*Including *Acmena* (11 species) and *Cleistocalyx* (21 species).

†These are *Jossinia* Commers. (Merrill 1950*b*; Diels 1922).

'abaxial'; this parenchyma is invariably located on the tangent of the vessel closest to the cambium and varies from a few cells to definite wing-like extensions. In some of these cases this parenchyma may be no more than the normal apotracheal diffuse, which by the abundance of vessels and the proximity of vasicentric tracheids, appears to be connected to the vessel. Metcalfe and Chalk (1950) and other wood anatomists have used abaxial or 'unilaterally paratracheal' parenchyma as a feature of diagnostic value. (This was discussed at a meeting of the International Association of Wood Anatomists held at the time of the Botanical Congress in Stockholm, 1950.) In the Myrtaceae, however, the authors have found that this feature must be used with care, and in Table 2 it has only been included to indicate where the tendency to this arrangement is most evident. Metcalfe and Chalk mention this arrangement as occurring in *Calyptranthes* (1 species), *Eugenia* p.p., *Kjellbergiodendron, Melaleuca* p.p., and *Myrtella.*

Metcalfe and Chalk point out that the parenchyma of the family as a whole is of two intergrading types (i) predominantly apotracheal; diffuse to irregular uniseriate bands in most of the genera with solitary pores, and (ii) predominantly paratracheal in genera in which pore multiples are relatively common. This, as a broad trend, is correct but Table 2 shows that there are many exceptions.

Mention has been made in the literature of the occasional presence of scalariform perforation plates and opposite vessel pitting in *Myrceugenia apiculata* (DC.) Ndzu. (Record and Hess 1943) and in *Myrceugenia, Myrtus communis* L., and *Eugenia* (1 species) (Metcalfe and Chalk 1950); and of the presence of spiral thickenings in the above genera p.p. (Metcalfe and Chalk 1950; Janssonius 1908). In the material examined (including two samples of *Myrtus communis* L.) no sign of scalariform perforation plates, opposite pitting, or spirals in the vessels has been observed.

It is interesting to speculate on the diversity in anatomy of the large genus *Eucalyptus,* as against the remarkable similarity of the species of the genus *Syzygium* which, in point of numbers (over 900) exceeds *Eucalyptus. Syzygium,* though widely distributed over tropical Asia, Malaysia, and the Pacific, has, in common with many other genera of a number of families from this region which are characteristic of the primary forests, a high percentage of local endemism; and like many of such genera, e.g. *Elaeocarpus, Canarium, Ficus,* etc., shows a remarkable resemblance between species. *Eucalyptus,* although practically confined to the continent of Australia, has evolved in many forms, tall trees to mallee, to suit a wide series of habitats from rain-forest to savannah and areas of low rainfall.

The distribution of the genera covered by this work is given in Table 5; showing the number of species of each found in particular localities throughout the area under consideration. Where these species figures are unknown or approximate they are indicated by a query (?). However, the table serves to show the broad trends of distribution of the genera dealt with in this work. It indicates also the two most important centres of distribution: (1) Australia and, to a lesser degree, New Guinea (*Decaspermum* and *Xanthomyrtus*) and

(2) New Caledonia with *Xanthostemon, Piliocalyx, Pleurocalyptus,* and *Spermolepis,* of which the three latter are endemic.

Apart from the tribe Chamaelaucieae, which includes 13 endemic genera not considered in this work, Australia has 10 genera endemic to the continent and four others (*Baeckia, Eucalyptus, Leptospermum, Melaleuca*) with all but a few species endemic.

As the Lecythidaceae (including the Barringtoniaceae) was at one time included with the Myrtaceae, it is of value to review briefly the major wood anatomical differences between the families. These are set out below:

Myrtaceae	Lecythidaceae
1. All genera except *Eugenia B, Piliocalyx, Eucalyptopsis,* and *Xanthomyrtus* characterized by fibres with conspicuously bordered pits	1. Fibres with simple to inconspicuously bordered pits
2. Pitting of vessels and tracheary elements vestured in all genera	2. Vestured pits absent
3. Vasicentric tracheids present in all genera except *Eugenia B, Piliocalyx,* and *Eucalyptopsis*	3. Vasicentric tracheids absent
4. Vessels predominantly to exclusively solitary except in *Eucalyptus B, Angophora,. Eugenia B, Piliocalyx, Eucalyptopsis,* and *Xanthomyrtus*	4. Vessels in radial multiples, frequently 2-4 and sometimes up to 6, clusters common in most genera
5. Diffuse parenchyma present in all genera except *Eugenia B* and *Piliocalyx*; sometimes both apotracheal and paratracheal in the one wood; confluent bands only in *Eugenia B, Piliocalyx, Angophora, Eucalyptus B, Eucalyptopsis, Spermolepis,* and *Kjellbergiodendron*	5. Parenchyma in narrow to wide bands either paratracheal or apotracheal

Although the Myrtaceae can readily be distinguished from the Lecythidaceae by the presence of vestured pitting and, with the exception of one or two genera, on several other features, as indicated above, it is interesting to note that the group *Eugenia B* and *Piliocalyx* of the Eugeniinae shows some resemblance to *Barringtonia* of the Lecythidaceae. This genus has a preponderance of paratracheal, confluent parenchyma, and vessel-ray pitting similar to the *Eugenia B* group.

When considering other families, characterized by vestured pitting, which might be confused with the Myrtaceae on microscopic features, this family is best split into two main groups:

(1) Genera having vessels predominantly in multiples, paratracheal, confluent parenchyma, heterogeneous rays, and scalariform vessel-ray pitting, and

(2) Genera with predominantly solitary vessels, fibre tracheids, and vasicentric tracheids.

Under (1) the only other families with this combination of features are the Melastomaceae and the Lythraceae of the Myrtales (B & H) and the

Vochysiaceae. In the Melastomaceae only the subfamily Melastomoideae and *Astronia* and *Astronidium* have such features. The Astroniae, with the above two generic exceptions, and the Memecyleae have fibre tracheids and included phloem. The majority of genera in the Melastomoideae, however, have septate fibres and the few without have predominantly uni- or biseriate rays with few procumbent cells.

The Lythraceae are also distinct in having septate fibres, with the exception of *Pemphis,* but this differs from the *Eugenia B* group in having small vessel-ray pitting similar to the inter-vessel type.

The Vochysiaceae, although taxonomically unrelated to the Myrtaceae, have intercellular canals of the vertical traumatic type similar to the group *Eucalyptus, Angophora,* and *Spermolepis,* but these are not found in the *Eugenia B* group.

Under (2) above the only family with similar features is the Dipterocarpaceae (excluding the subfamily Monotoideae). This family is, however, characterized by the presence of normal vertical canals of the schizogenous type whereas the canals or gum 'veins' occurring in *Eucalyptus, Angophora,* and *Spermolepis* are of the traumatic type. Vertical canals are absent from the remainder of the Myrtaceae.

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Explanation of Plates 1-10

Plate 1

Fig. 1.—*Rhodamnia trinervia* Bl. Transverse section showing solitary vessels, apotracheal parenchyma, and two distinct widths of ray. × 25.

Fig. 2.—*Rhodamnia sessiliflora* Benth. Transverse section showing apotracheal diffuse to banded parenchyma. × 25.

Fig. 3.—*Austromyrtus hillii* (Benth.) Burret. Transverse section showing extremely small, solitary vessels. × 25.

Fig. 4.—*Lophomyrtus bullata* Burret. Transverse section showing small, solitary vessels, and apotracheal, diffuse parenchyma. × 25.

Fig. 5.—*Decaspermum paniculatum* (Lindl.) Kurz. Transverse section showing solitary, oval pores and sparse, diffuse parenchyma. × 25.

Fig. 6.—*Rhodomyrtus psidioides* Benth. Transverse section showing variation in vessel size. × 25.

Plate 2

Fig. 1.—*Eugenia grisiana* Guillem. Transverse section showing small, solitary vessels, and apotracheal, diffuse to banded parenchyma. × 25.

Fig. 2.—*Cleistocalyx seemani* (A. Gray) Merr. & Perry. Transverse section showing vessels in radial multiples, and paratracheal confluent parenchyma. × 25.

Fig. 3.—*Cleistocalyx gustavioides* (F. M. Bail.) Merr. & Perry. Transverse section showing vessels in radial multiples, and paratracheal, confluent parenchyma in regular bands. × 25.

Fig. 4.—*Eugenia maire* A. Cunn. (*Eugenia B*). Transverse section showing vessels in radial multiples and clusters; parenchyma abundant in irregular, wide, confluent bands. × 25.

Fig. 5.—*Acmena brachyandra* (Maid. & Betche) Merr. & Perry. Transverse section showing vessels in radial multiples, and paratracheal, confluent parenchyma. × 25.

Fig. 6.—*Syzygium decipiens* (Koord. & Val.) Merr. & Perry. Transverse section showing rays of two widths and sparse, paratracheal to aliform parenchyma. × 25.

PLATE 3

Fig. 1.—*Backhousia bancroftii* Bail. & F. Muell. Transverse section showing solitary vessels and apotracheal parenchyma tending to link up into tangential irregular bands. × 25.

Fig. 2.—*Backhousia citriodora* F. Muell. Transverse section showing small, solitary vessels and diffuse parenchyma; note band of parenchyma at top. × 25.

Fig. 3.—*Metrosideros robusta* A. Cunn. Transverse section showing variation in vessel size and sparse, apotracheal parenchyma. × 25.

Fig. 4.—*Metrosideros umbellata* A. Rich. Transverse section showing vessel and parenchyma distribution. × 25.

Fig. 5.—*Tepualia stipularis* Gris. Transverse section showing small, solitary vessels and paratracheal and diffuse parenchyma. × 25.

Fig. 6.—*Tristania pachysperma* (F. Muell. & F. M. Bail.) Francis. Transverse section showing vessel and parenchyma distribution. × 25.

PLATE 4

Fig. 1.—*Syncarpia hillii* F. M. Bail. Transverse section showing solitary vessels and apotracheal, diffuse parenchyma. × 25.

Fig. 2.—*Choricarpia leptopetala* (F. Muell.) Domin. Transverse section showing oblique zoning of vessels and apotracheal parenchyma tending to be grouped tangentially. × 25.

Fig. 3.—*Lysicarpus angustifolius* (Hook.) Druce. Transverse section showing solitary vessels, uniseriate rays, and sparse, diffuse parenchyma. × 25.

Fig. 4.—*Tristania conferta* R. Br. Transverse section showing solitary, tylosed vessels. × 25.

Fig. 5.—*Tristania exiliflora* F. Muell. Transverse section showing vessels with numerous deposits, and abundance of diffuse parenchyma. × 25.

Fig. 6.—*Eucalyptus deglupta* Bl. Transverse surface of wood showing marked oblique arrangement of solitary vessels. × 10.

PLATE 5

Fig. 1.—*Angophora intermedia* DC. Transverse section showing vessels in radial multiples, abundant tyloses, and paratracheal, aliform to confluent parenchyma. × 25.

Fig. 2.—*Eucalyptus corymbosa* Sm. Transverse section showing radial multiples and clusters of vessels and aliform to confluent parenchyma. × 25.

Fig. 3.—*Eucalyptus goniocalyx* F. Muell. Transverse section showing large, solitary vessels and abundance of paratracheal parenchyma, also diffuse. × 25.

Fig. 4.—*Eucalyptus macrorrhyncha* F. Muell. Transverse section showing moderately small vessels, sparse parenchyma, and distinct rays due to abundance of deposits. × 25.

Fig. 5.—*Eucalyptus obliqua* L'Hérit. Transverse section showing typical strong oblique alignment of vessels and sparseness of deposits in the rays.

Fig. 6.—*Spermolepis gummifera* Brongn. & Gris. Transverse section showing large, solitary vessels and confluent parenchyma, also apotracheal, diffuse. × 25.

PLATE 6

Fig. 1.—*Leptospermum scoparium* Forst. Transverse section showing definite growth rings marked by dense band of fibres and fewer vessels. × 25.

Fig. 2.—*Agonis flexuosa* Lindl. Transverse section showing vessel distribution and paratracheal and diffuse parenchyma. × 25.

Fig. 3.—*Callistemon salignus* DC. Transverse section showing marked growth rings, small, solitary vessels, and diffuse parenchyma. × 25.

Fig. 4.—*Melaleuca leucadendron* L. Transverse section showing variable vessel size and apotracheal parenchyma in short, irregular bands. × 25.

Fig. 5.—*Eucalyptus gigantea* Hook. f. Transverse section showing band of vertical canals or 'gum vein.' × 25.

Fig. 6.—*Eucalyptus gigantea* Hook. f. Transverse surface of wood showing thick-walled late wood fibres and lack of vessels in first-formed early wood. × 10.

PLATE 7

Fig. 1.—*Decaspermum paniculatum* (Lindl.) Kurz. Transverse section showing large, distinctly bordered fibre pits. × 500.

Fig. 2.—*Eugenia clusiaefolia* A. Gray. Tangential longitudinal section showing vestured pitting of vessels. × 800.

Fig. 3.—*Tristania suaveolens* Sm. Radial section of ray showing procumbent cells with silica bodies embedded in extraneous material. × 450.

Fig. 4.—*Eucalyptus obliqua* L'Hérit. Radial longitudinal section showing vasicentric tracheids. × 220.

Fig. 5.—*Tristania merguensis* Griff. Transverse section showing location of parenchyma chiefly on abaxial side of vessels. × 90.

Fig. 6.—*Rhodamnia trinervia* Bl. Transverse section showing multiseriate and uniseriate rays and parenchyma distribution. × 90.

PLATE 8

Fig. 1.—*Leptospermum scoparium* Forst. Radial section showing small vessel-ray pits similar to vessel pitting (type 1). × 400.

Fig. 2.—*Tristania conferta* R. Br. Radial section showing small, apparently simple vessel-ray pits (type 2). × 400.

Fig. 3.—*Syzygium onesimum* Merr. & Perry. Radial section showing apparently simple rounded, elongated to scalariform vessel-ray pits (type 3). × 400.

Fig. 4.—*Angophora intermedia* DC. Radial section showing large, apparently simple, rounded to oval vessel-ray pits (type 4). × 400.

Fig. 5.—*Spermolepis gummifera* Brongn. & Gris. Radial section showing type 4 (eucalyptian) vessel-ray pitting. × 400.

Fig. 6.—*Eucalyptus obliqua* L'Hérit. Radial section showing vessel-ray pitting characteristic of the genus. × 400.

Fig. 7.—*Melaleuca leucadendron* L. Radial section showing vessel-ray pitting in this species approaching type 4. × 400. (Remainder of genus type 2; see Fig. 2.)

PLATE 9

Fig. 1.—*Metrosideros robusta* A. Cunn. Tangential section showing heterogeneous rays. × 90.

Fig. 2.—*Eugenia maire* A. Cunn. Tangential section showing heterogeneous rays, and rays of two types, uniseriate and multiseriate. × 90.

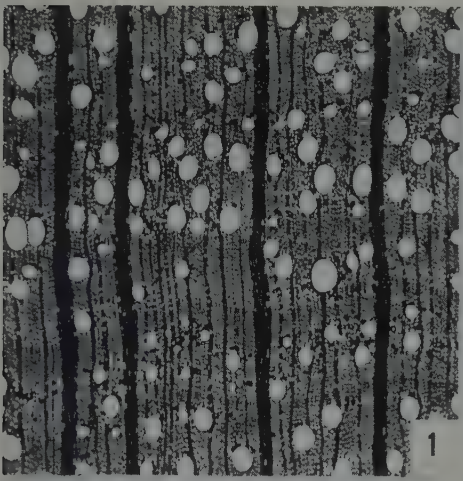
Fig. 3.—*Eucalyptus saligna* Sm. Tangential section showing low rays of one type, weakly heterogeneous, characteristic of majority of genera of the Leptospermoideae. × 90.

Fig. 4.—*Eugenia corynantha* F. Muell. Longitudinal section showing crystals in chambered parenchyma cells. × 220.

Fig. 5.—*Rhodamnia cinerea* Jack. Longitudinal section showing solitary, elongated crystals in parenchyma cells. × 220.

Fig. 6.—*Leptospermum ericoides* A. Rich. Tangential section showing solitary, large crystals in vertical series of parenchyma. × 220.

WOOD ANATOMY OF THE MYRTACEAE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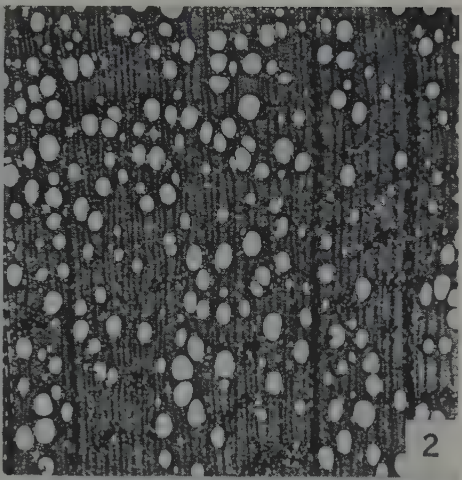
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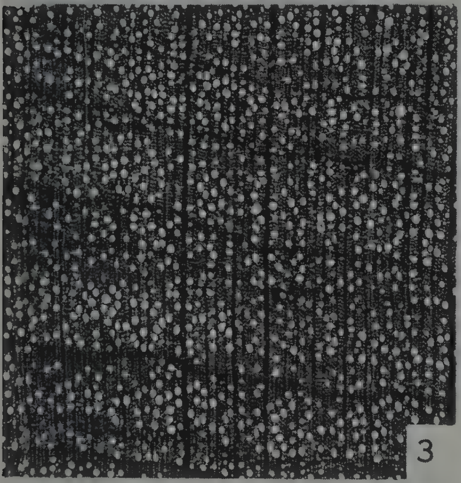
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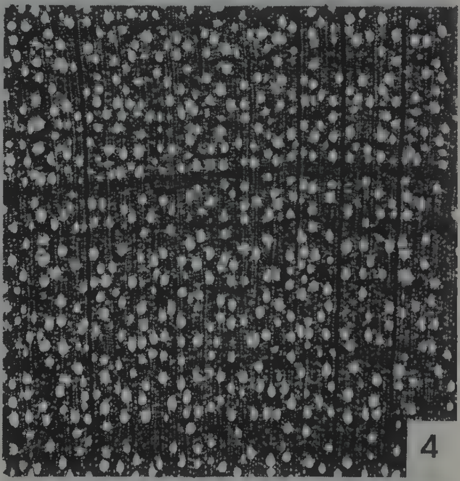
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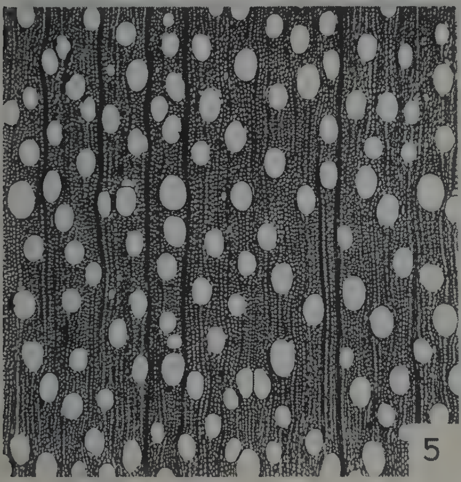
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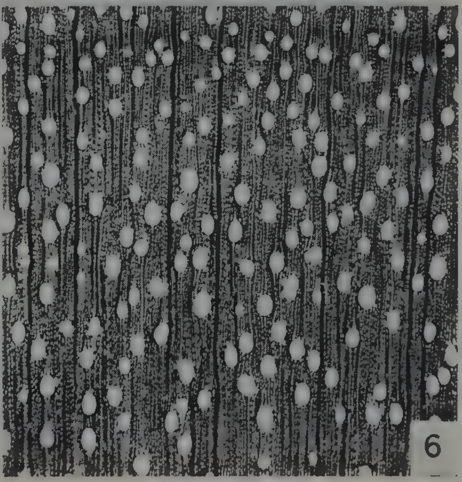
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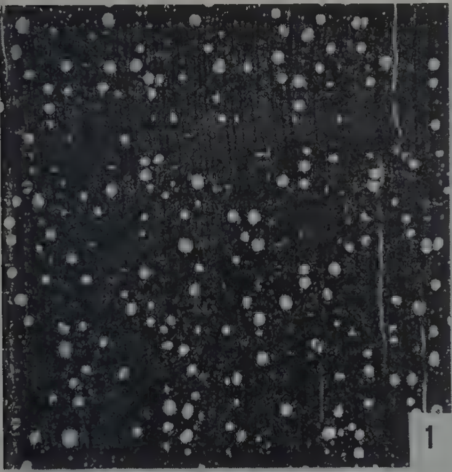
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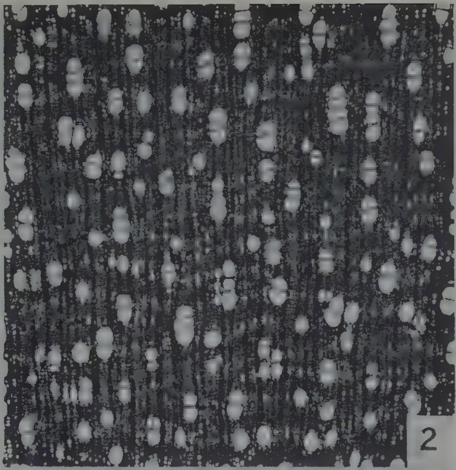
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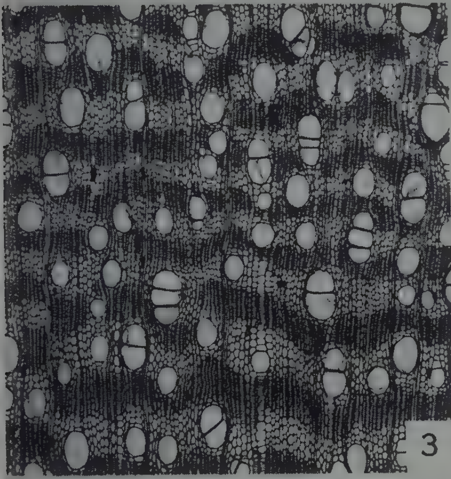
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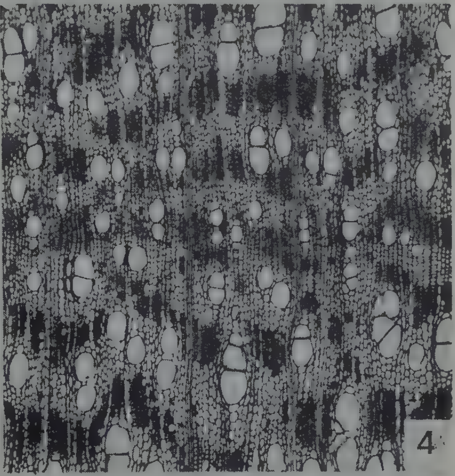
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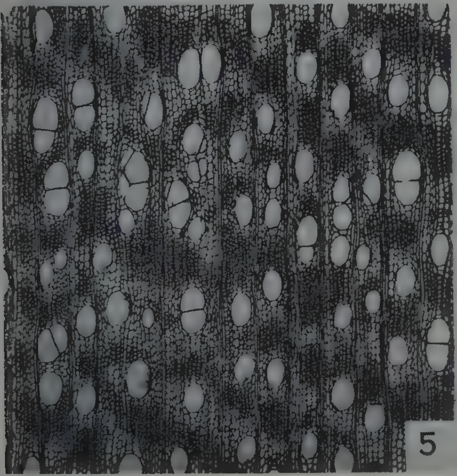
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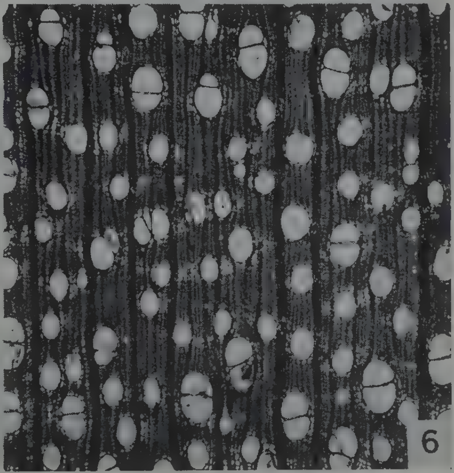
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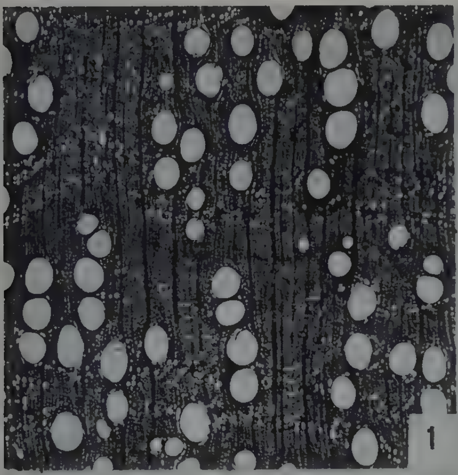

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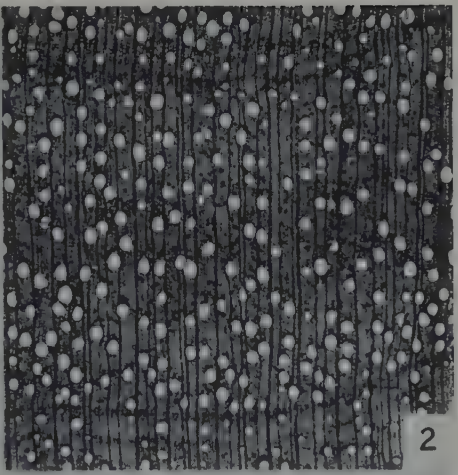

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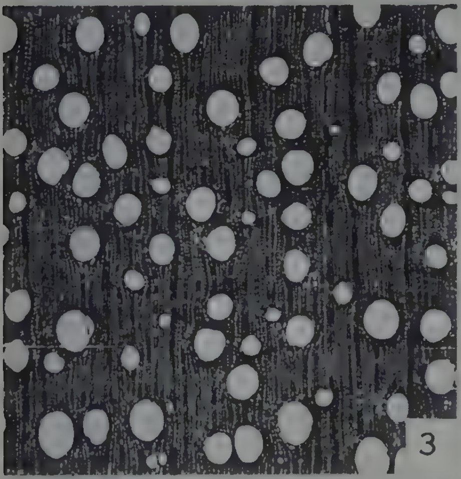

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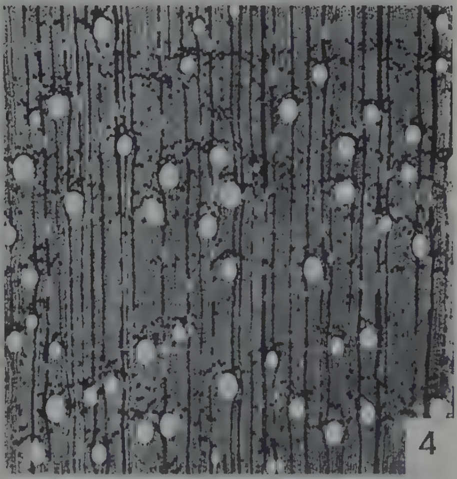

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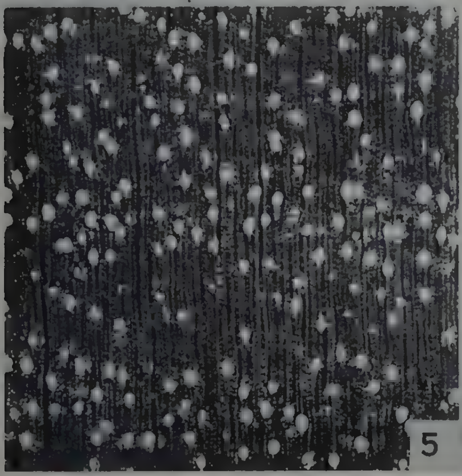

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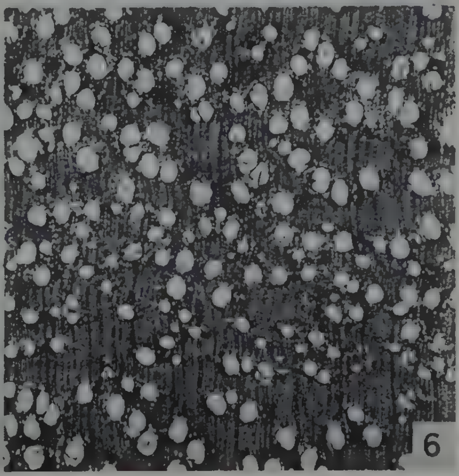

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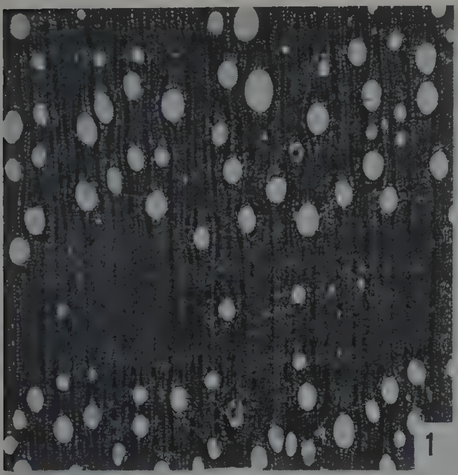
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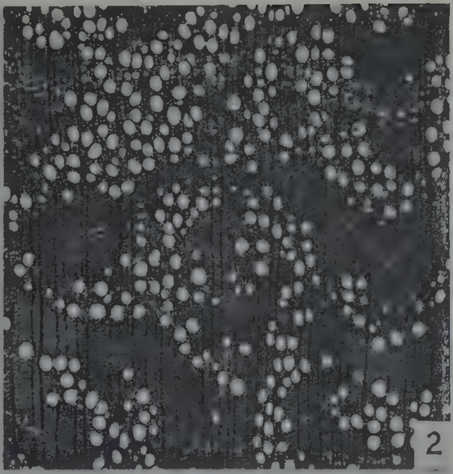
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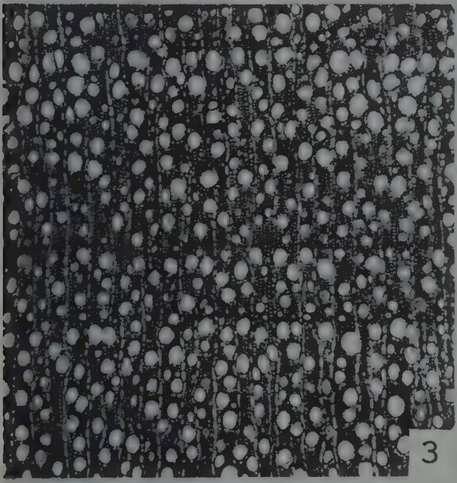
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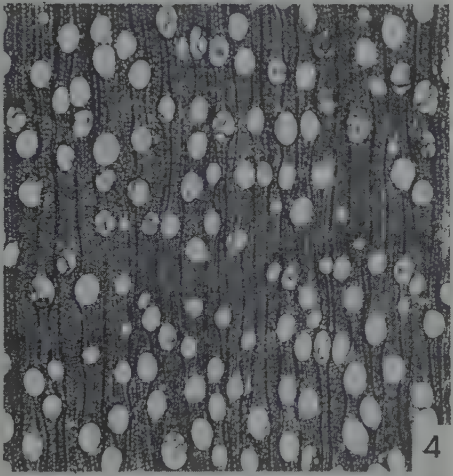
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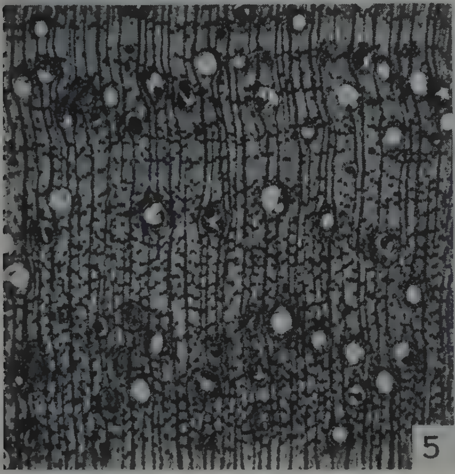
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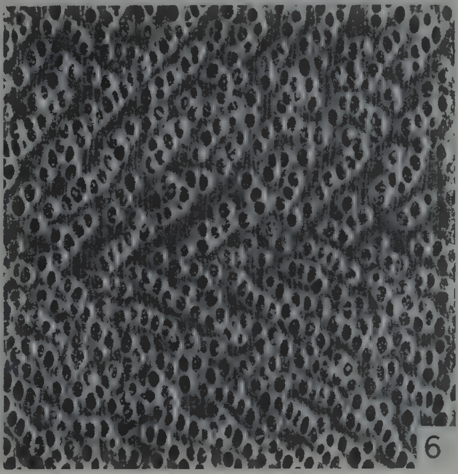
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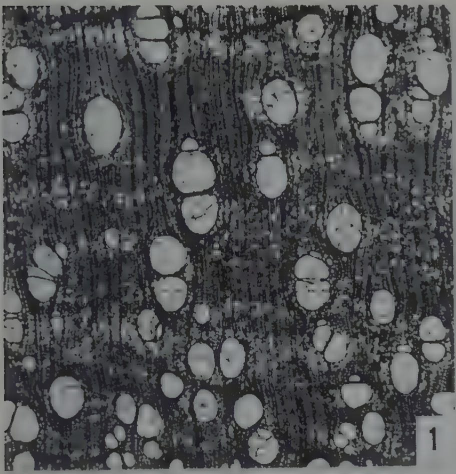
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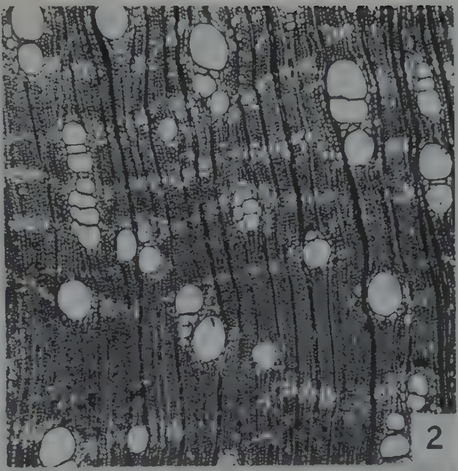
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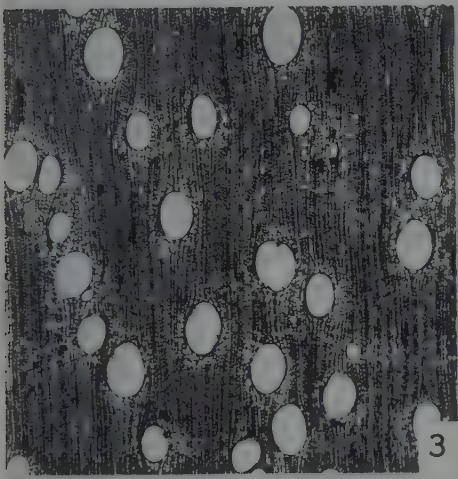
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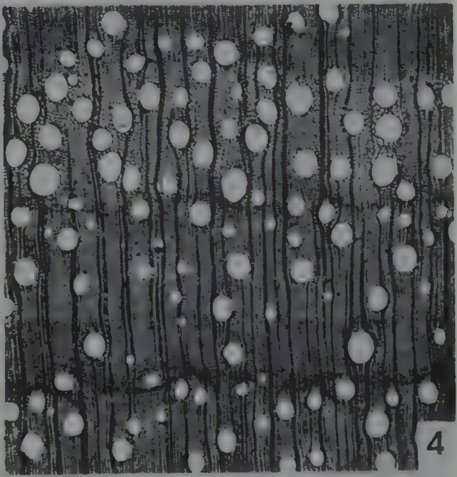
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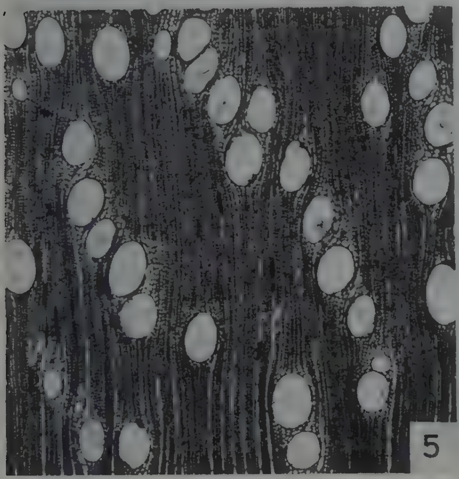
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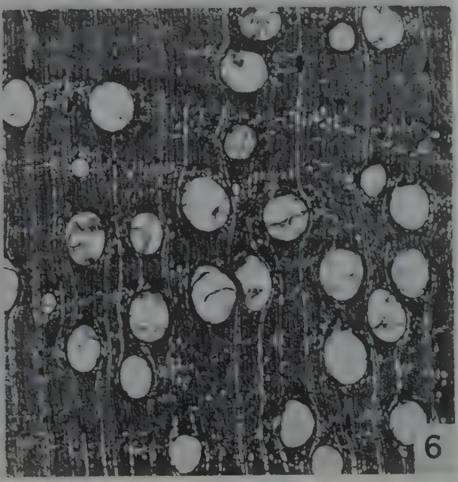
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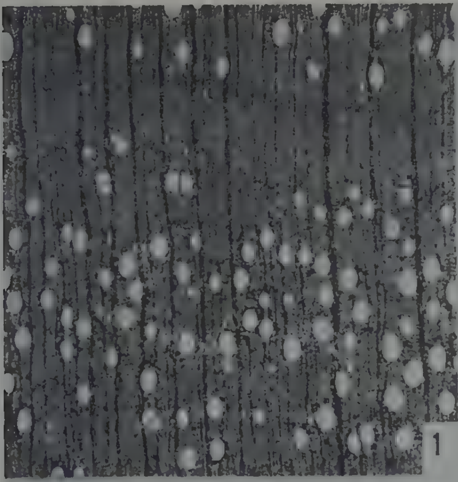

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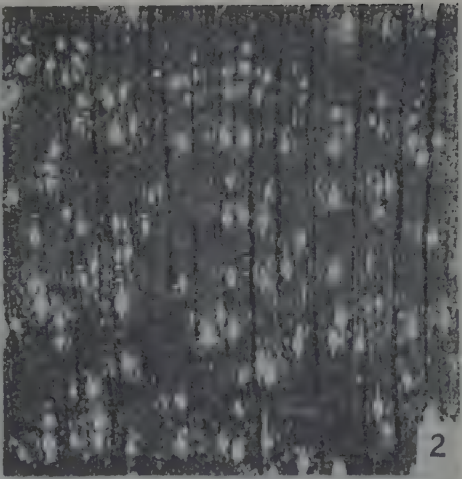

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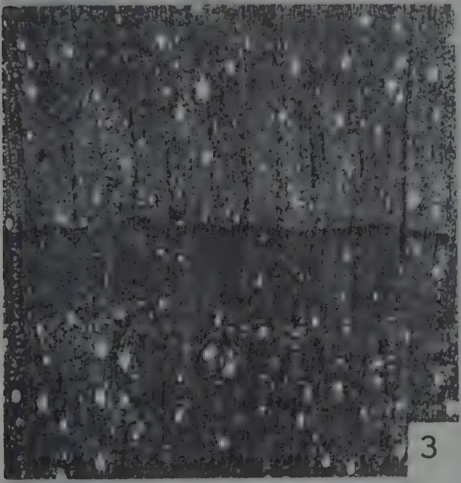

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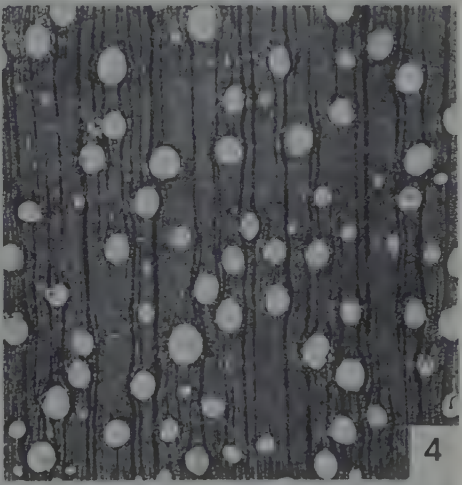

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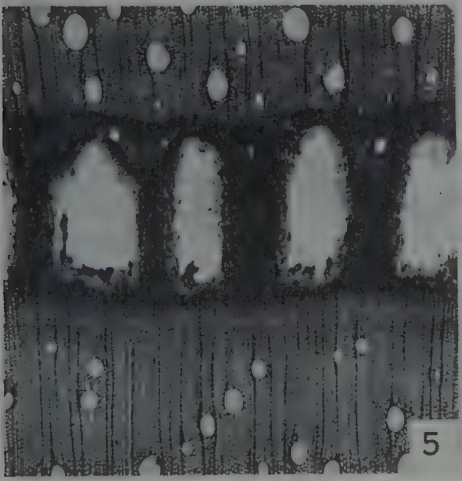

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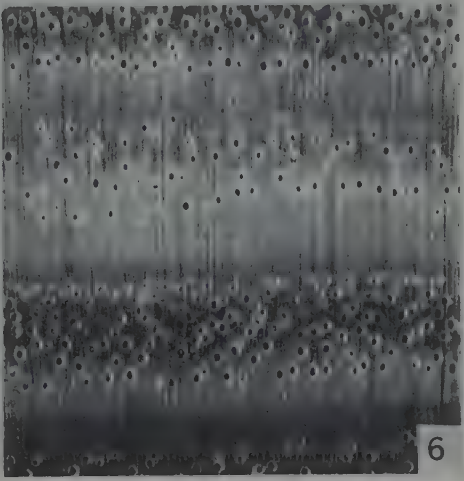

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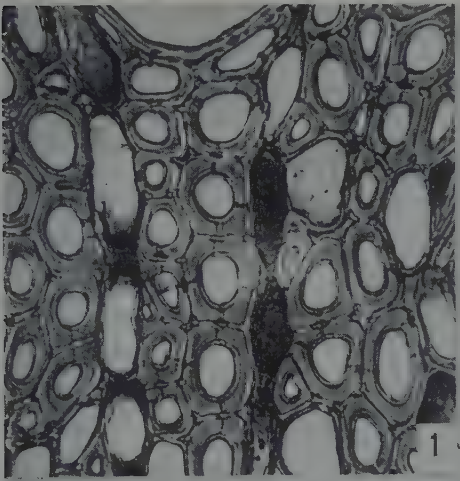
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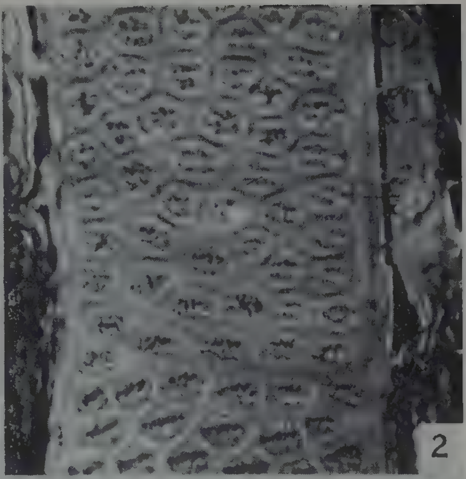
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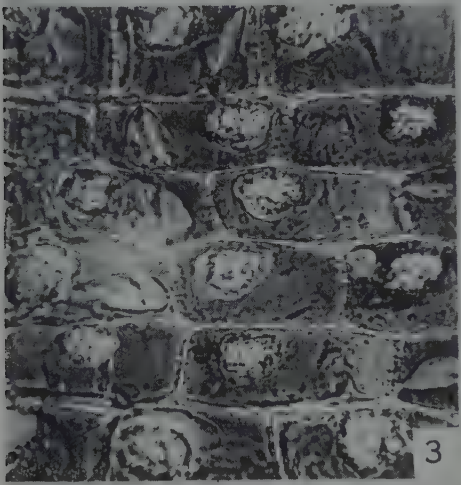
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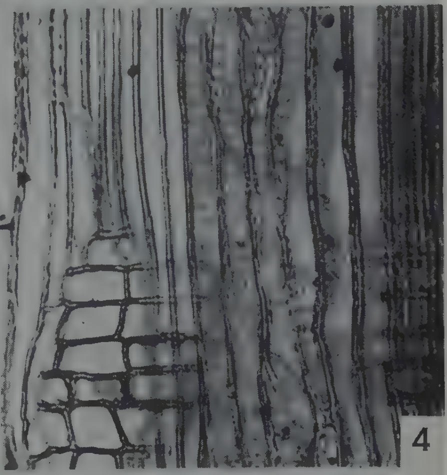
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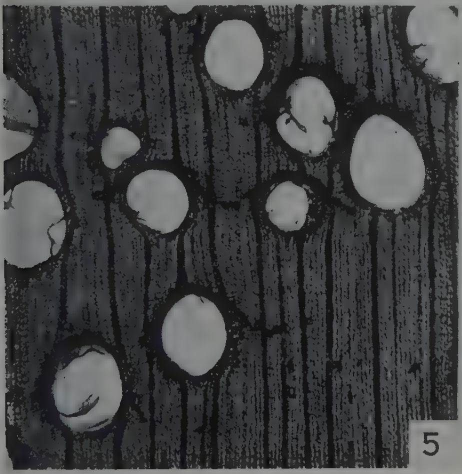
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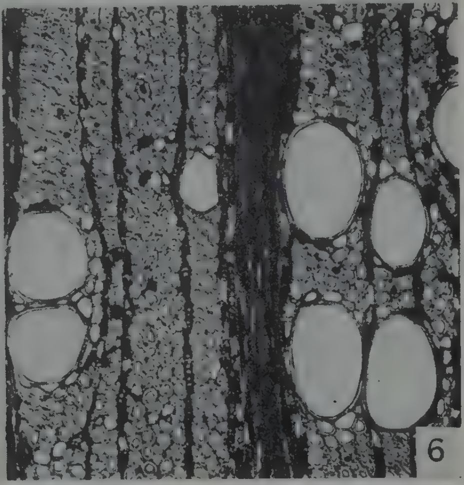
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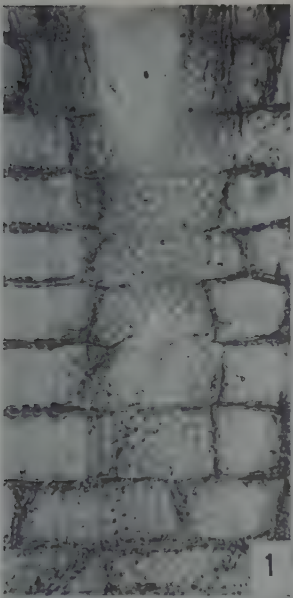
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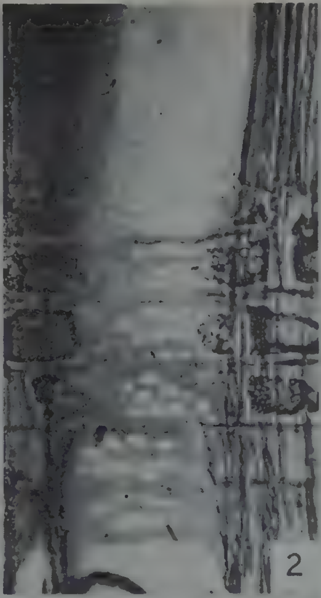
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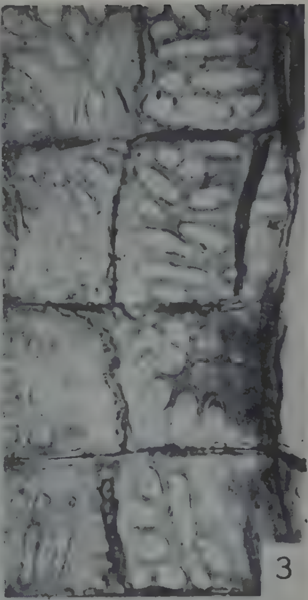
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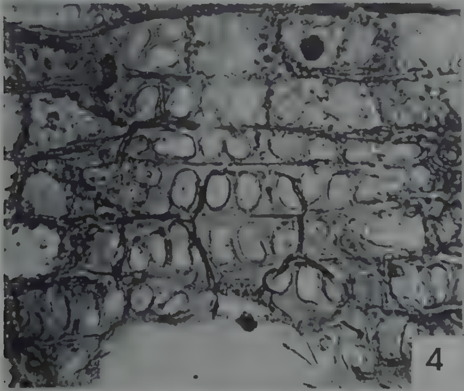
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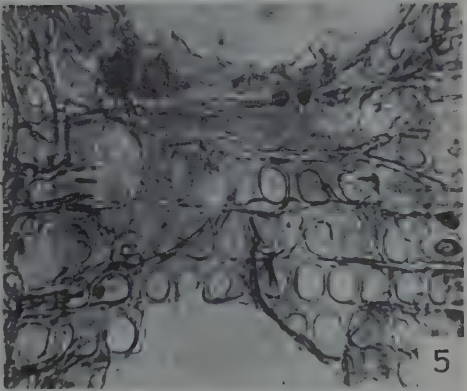
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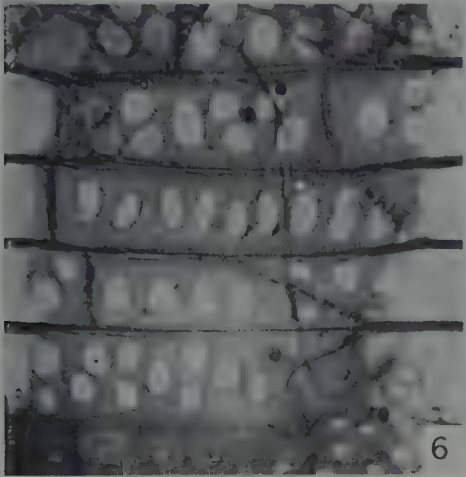
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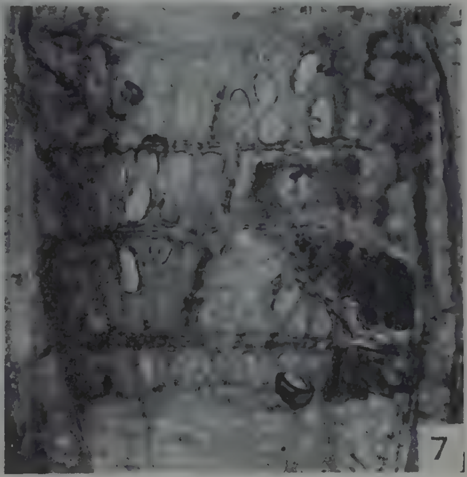
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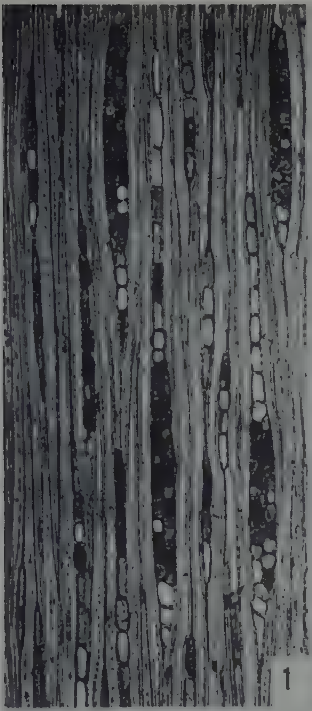
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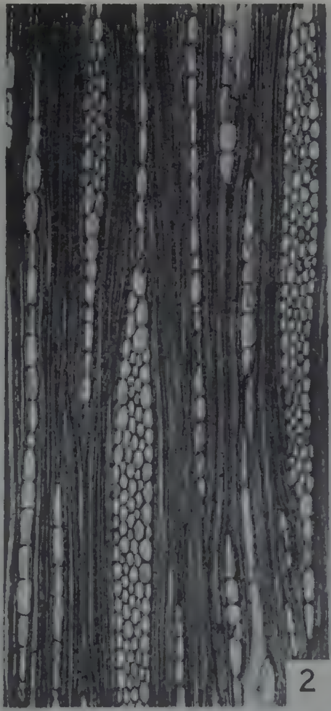
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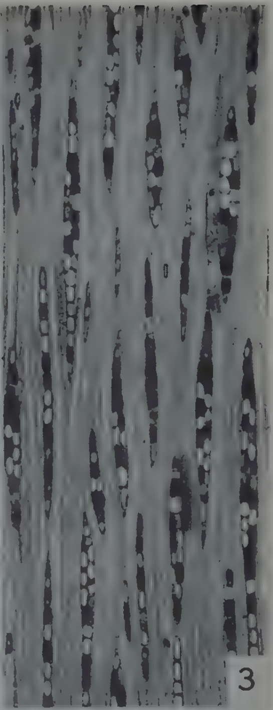
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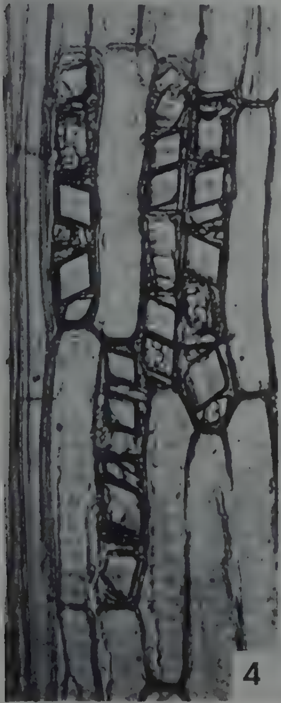
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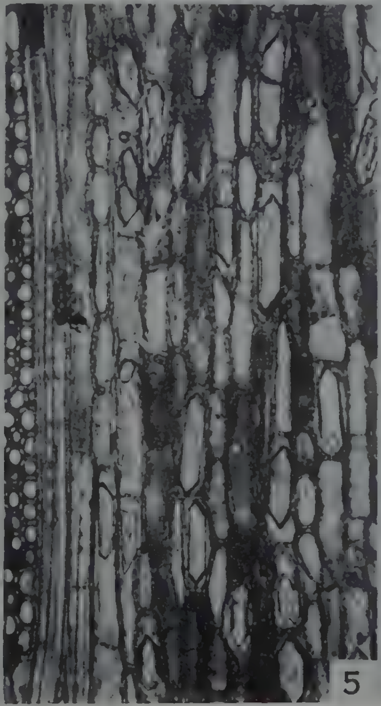
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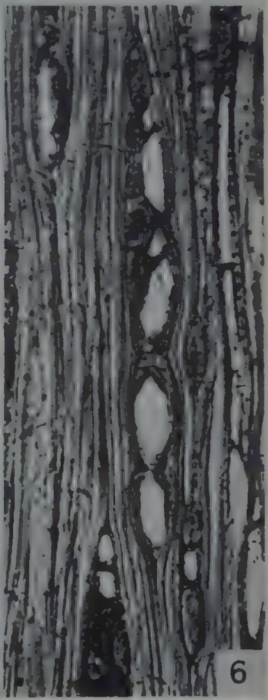
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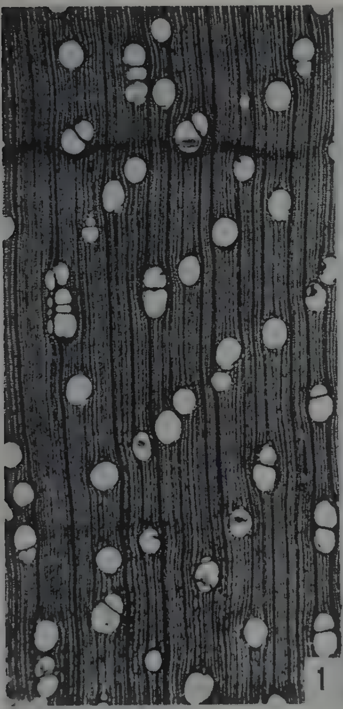

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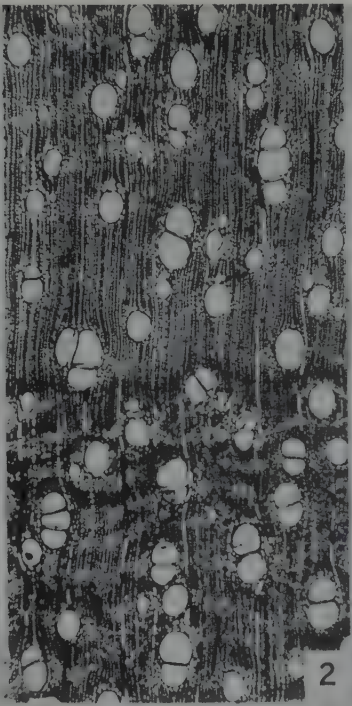

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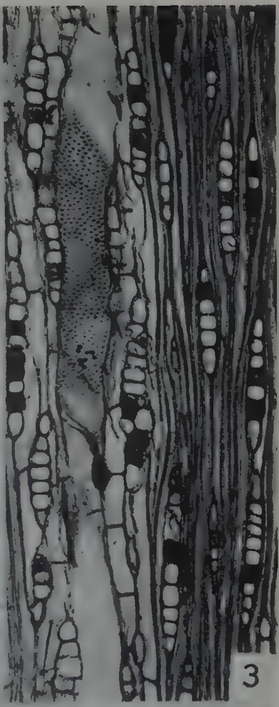

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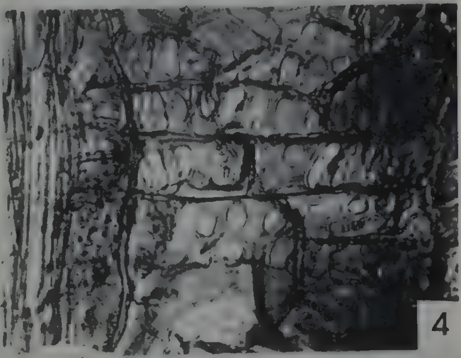

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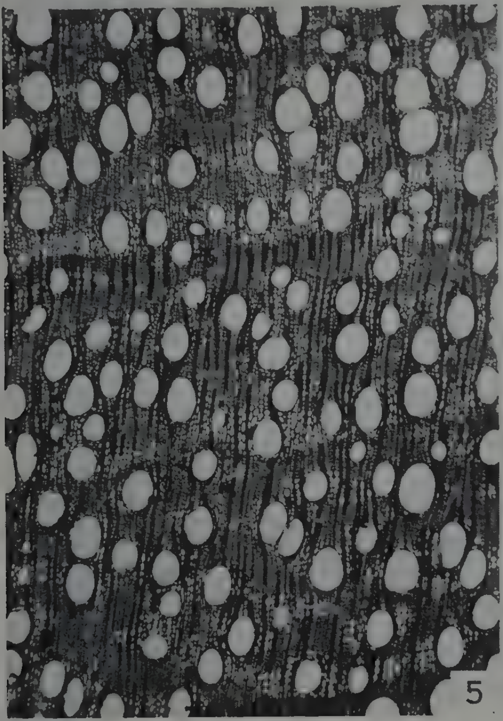

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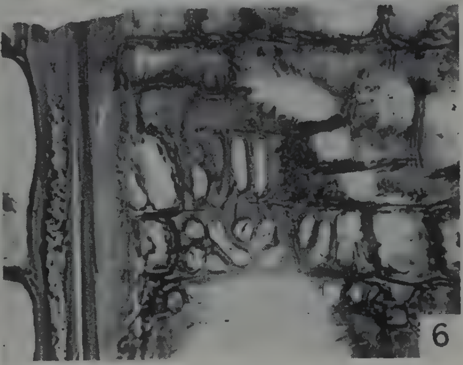

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Plate 10

Fig. 1.—*Eucalyptopsis* sp. aff. *E. papuana* C. T. White. Transverse section showing pore distribution and sparse, paratracheal parenchyma. × 25.

Fig. 2.—*Eucalyptopsis papuana* C. T. White. Transverse section showing paratracheal, aliform to confluent parenchyma. × 25.

Fig. 3.—*Eucalyptopsis papuana* C. T. White. Tangential longitudinal section showing low, predominantly uniseriate rays. × 90.

Fig. 4.—*Eucalyptopsis papuana* C. T. White. Radial longitudinal section showing vessel-ray pitting. × 320.

Fig. 5.—*Kjellbergiodendron limnogeiton* Burret. Transverse section showing pore size and distribution and abundant paratracheal, confluent parenchyma. × 25.

Fig. 6.—*Kjellbergiodendron hylogeiton* Burret. Radial longitudinal section showing characteristic scalariform vessel-ray pitting. × 320.

THE ANATOMY OF BARK

I. THE GENUS *EUCALYPTUS*

By M. Margaret Chattaway*

[*Manuscript received November 25, 1952*]

Summary

The most characteristic microscopic features of the bark of over 150 species of *Eucalyptus* are described.

The structure of the phloem and cortex of the eucalypt twig, the changes that occur with increasing diameter, and the differences between the deciduous and persistent barks are described and illustrated.

The detailed structure of the fully developed bark and the development of features characteristic of some of the most distinctive bark types have been studied, especially in the following groups: *Corymbosae* and *Corymbosae-peltatae, Transversae, Exsertae* and *Sub-exsertae, Globulares, Viminales, Pachyphloiae, Fraxinales, Longitudinales, Piperitales, Psathyroxyla, Buxeales, Siderophloiae.*

I. Introduction

Although a considerable amount of research has been done on the chemistry of bark and on its utilization there appears to be very little recent literature on its development and structure. The early work is summarized by de Bary (1884) and Solereder (1908); Metcalfe and Chalk (1950) give brief details of bark in the general resumé of the characters of the different families, but there is still very little detailed information to be obtained. The eucalypts have been almost completely neglected in this respect, for although features characteristic of the different barks have given rise to the vernacular names of some of the subdivisions of the genus, as in the stringybarks and ironbarks, yet these names were given on the external appearance of the barks and little work has been done on their development or on the fundamental differences between the groups.

The structural differences between xylem and phloem are due not only to the different functions the tissues fulfil, but also to their different positions in relation to cambial growth and the increase in girth of the stem. As the increase that results from cambial growth is on the outside of the xylem this tissue undergoes little extension after it has been formed, and secondary thickening of the cell walls soon fixes it into a mould that does not alter much throughout its life. Such is not the case in the phloem. The cambial divisions, which are sufficient to keep pace with the increasing perimeter on the inner edge of the phloem, cannot have any effect at the point of greatest increase, which is in the oldest layers of the phloem, on the outside of the stem, at the farthest point from the actively growing cambium.

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* Division of Forest Products, C.S.I.R.O., South Melbourne.

The phloem is, therefore, constantly stretching tangentially throughout its life, and the cells of the phloem parenchyma and phloem rays remain meristematic and undergo division and enlarge until they are finally isolated by the formation of a periderm, which cuts them off from the food supply and causes their death and the subsequent formation of rhytidome.

II. Definitions

The term bark is loosely used in the timber trade to mean the outer covering of the stem, and to include everything outside the cambial layer. In botanical usage, however, the tissues outside the cambium comprise, in a young stem, the *secondary* phloem, which is formed by the cambium in the same way as the secondary wood, the *primary* phloem, *cortex*, and *epidermis*.

In older stems the increasing diameter causes extension, and finally rupture of the epidermis, the place of which is taken by a *periderm*. This consists of three layers, the *phellogen* or cork cambium, which acts in the same way as the cambial layer of the stem, cutting off layers of cells on both sides. The layers towards the outside are known as the *phellem* or cork, and those towards the inside are known as the *phelloderm*. Further expansion of the stem causes the periderm to rupture, and its place is taken by another deeper-seated periderm. Each periderm layer cuts off from food and water supplies all the tissues to the outside, so that as soon as a new periderm forms changes occur in the tissue outside it, which ultimately cause it to die. These dead tissues make up the *rhytidome,* or bark in the strict sense.

The many different uses of the word *bark* have led to so much confusion that it appears best to retain this term in its non-technical sense to designate all the tissues outside the cambium, and to use throughout this paper the more specific terms described above, the term *rhytidome* being adopted to indicate the alternate layers of periderm and dead cortical or phloem tissues.

For convenience of reference these terms are briefly defined below:

Primary wood and primary phloem.—First-formed xylem or phloem, differentiated from an apical meristem.

Secondary wood and secondary phloem.—The wood and phloem formed by the cambium.

Cortex.—The layer or layers of tissue surrounding the wood and phloem.

Epidermis.—The outer layer of the stem, often with strongly thickened and cuticularized outer walls.

Lenticel.—An area of loosely connected tissue forming a breathing pore in very young stems.

Periderm.—The layers which replace the epidermis as the impermeable covering of older stems.

Phellogen.—The meristematic layer of the periderm.

Phellem or cork.—The outer layers of the periderm } cut off by
Phelloderm.—The inner layers of the periderm } the *phellogen.*

Rhytidome.—The dead layers of cork enclosing pockets or layers of dead cortical or phloem tissue.

III. Material Examined

One hundred and fifty-five different species of *Eucalyptus* have been examined. They are listed in Appendix 1. For each species the number preceding the name refers to Blakely's classification of eucalypts (Blakely 1934) and the number in brackets that follows the name gives the number of samples available for examination; authorities for specific names are also given in this list.

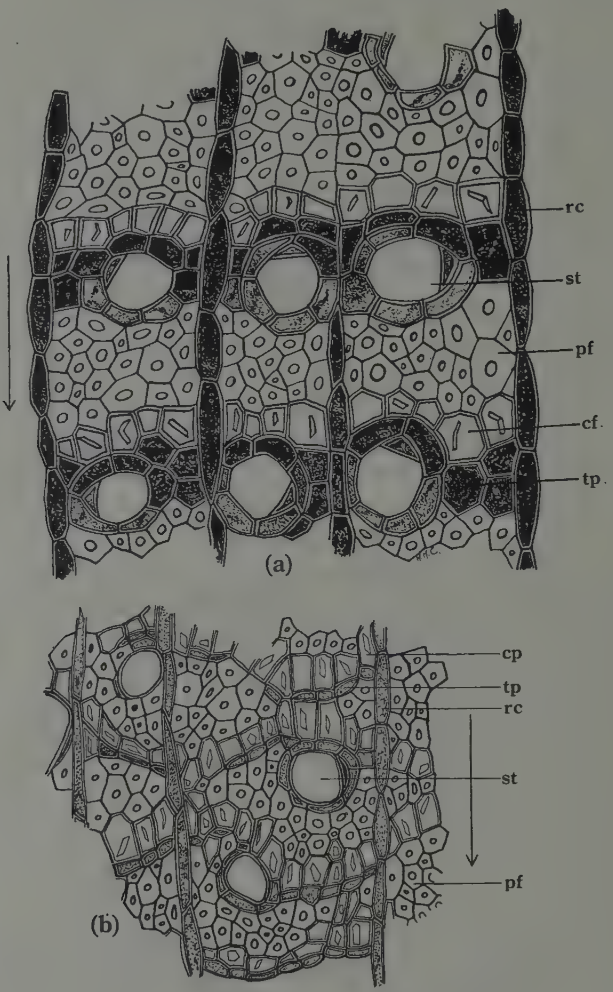


Fig. 1.—Details of phloem. (*a*) *E. obliqua.* (b) *E. scabra.* The arrow points towards the cambium in this and all subsequent figures. × 225. *cp,* crystalliferous parenchyma; *tp,* tanniniferous parenchyma; *rc,* ray cells; *st,* sieve tubes; *pp,* phloem parenchyma; *pf,* phloem fibres.

Many of these species were available only as single samples and therefore no attempt has been made to give detailed bark descriptions.

In some of the larger and better-represented groups, however, a definite pattern of bark structure becomes apparent; this is described and species differing from it are noted. A chart of special bark features, and the species in which they occur, is also given in Appendix 1.

IV. Young Bark

The structure of the twig and young stem is very uniform throughout the genus, only minor differences in detail having been observed in the species examined.

On cross section eucalypt twigs have a roughly four-angled pith, which sometimes contains a few stone-cells, surrounded by a ring of fibres. Outside these fibres is a ring of internal phloem and then the normal sequence of a young stem; xylem, phloem, and cortex (Plate 1, Fig. 1).

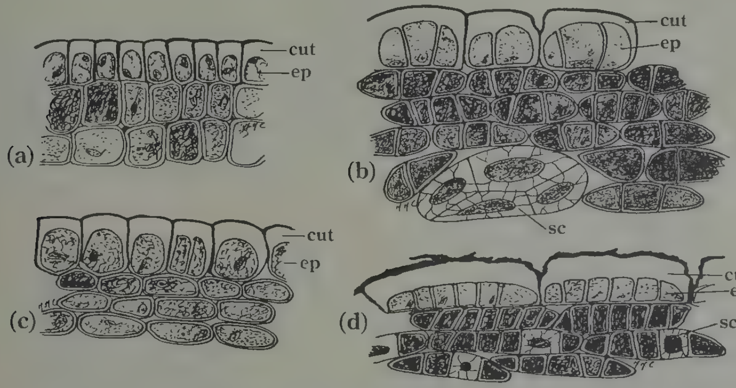


Fig. 2.—*E. gigantea,* cross section of epidermis and outer layers of the cortex. × 225. *cut,* cuticle; *ep,* epidermis; *sc,* stone-cells.

The phloem consists of sieve tubes and their companion cells and an accompanying layer of parenchyma; outside these is a layer of tanniniferous parenchyma; then a layer of rather large-celled crystalliferous parenchyma from which all traces of nucleus and protoplasm disappear immediately the cells are cut off from the cambial layer, and finally a band of fibres is formed, varying in width from one to five cells. This sequence is repeated throughout the secondary phloem. There is considerable variation in the width of the tanniniferous and crystalliferous layers, and in the size and shape of the fibre bundles, both between species and in different trees of the same species (Fig. 1 (*a*), (*b*)). The phloem rays vary in width in the different species; they are usually filled with tannins in solution. All the living parenchyma of the phloem contains abundant starch. The cortex consists of tanniniferous parenchyma, in the outer part of which occur a variable number of oil glands which are lined with a thin-walled epithelial layer (Plate 1, Figs. 1, 2, 3).

In very young stems the epidermis consists of a single layer of cells with the radial axes slightly longer than the tangential. The inner walls of these cells are thin, the radial and outer ones very thick and strongly suberized (Plate 1, Fig. 2).

The growth of the epidermis and outer cortex keeps pace with the increasing girth of the stem by radial divisions, the resultant cells at first retaining the general outline of the original mother cell. This is shown in Figure 2. In the epidermal layer the cuticle over each cell grows with the growing cell, and the final group may include six to eight daughter cells which are separated from the next group by the original radial extensions of the cuticle. The cortical cells undergo similar expansion, some of the daughter cells becoming thick-walled stone-cells (*sc* in Fig. 2 (*d*)).

Older stems show little change in the phloem, except for the addition of further sequences of sieve-tubes, parenchyma, and fibres. The effects of the greater girth caused by the secondary growth of the stem show themselves in the stretching of the soft tissue of the phloem and the tangential growth of the outer layers of the cortex (Plate 1, Fig. 3). It is in the cells of the cortex and epidermis that the greatest changes take place; the epidermal layer quickly becomes ragged and split as neither stretching nor division of the cells is as pronounced as in the cortical cells. The cortical parenchyma remains meristematic and forms a phellogen, which usually begins to develop first in association with the lenticels.

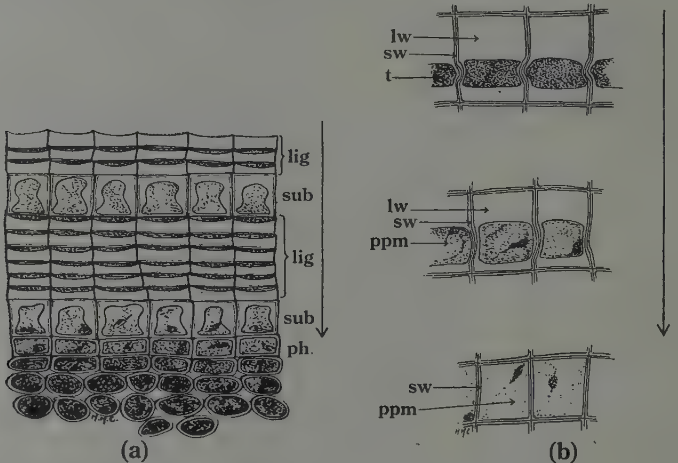


Fig. 3.—(*a*) *E. obliqua*. Details of periderm of smooth stem of young branch. × 225. *lig*, lignified layers of phellem; *sub*, suberized layers of phellem; *ph*, phellogen. (*b*) *E. botryoides*. Details of thickening of cells of suberized layer. × 320. *sw*, suberized wall; *lw*, lignified thickening; *t*, tannin-filled lumen of old cell; *ppm*, protoplasm and nucleus of younger cells.

This phellogen forms a periderm which is very similar in the young stems of all the eucalypts examined. Towards the phloem the cells that are cut off form one or more rows of approximately isodiametric cells (Plate 1, Fig. 4), sometimes heavily impregnated with tannin, occasionally containing chloroplasts and starch. Towards the outside of the stem the phellem is cut off; it consists of alternating layers of more or less isodiametric cells with suberized walls, and tangentially flattened cells with very thick lignified walls (Fig. 3 (*a*)).

The number of each of these cell rows varies from tree to tree and from place to place within a single tree. In young stems and in the smooth-barked species, the thickening of the lignified cells begins as soon as they are cut off by the phellogen, but it is often omitted altogether from the rough-barked species. The cells of the suberized layer are thin-walled when they are first formed, but later they acquire an inner lignified thickening (Fig. 3 (*b*)). This thickening is usually laid down unevenly around the cell, on the outer and inner tangential walls (Figs. 3 (*b*), 4 (*a*) lower; Plate 1, Fig. 5), or on the outer tangential and the radial walls (Figs. 3 (*a*), 4 (*a*) upper, 4 (*b*)). The thickening of the flattened lignified layer is usually laid on heavily on the inner tangential wall only (Figs. 3, 4), though occasionally there may be some thickening on both tangential walls. Differences have been observed even in the same species.

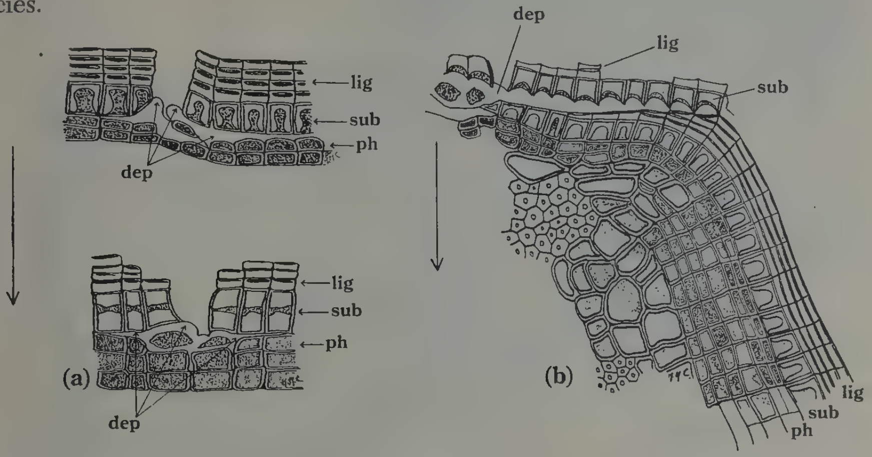


Fig. 4.—(*a*) Upper, *E. australiana*; lower, *E. regnans*. Suberin deposits secreted under cracks in the phellem. (*b*) *E. regnans*. Old and new periderms. All × 225. *lig*, lignified layers of phellem; *sub*, suberized layers of phellem; *ph*, phellogen; *dep*, suberin deposits.

As the young stem continues to expand, the first-formed periderm begins to be worn away, the flattened lignified cells of the phellem being rubbed off and the suberized layer splitting. These splits break the protective layer of the periderm and allow the cells underneath access to the air. The cells of the underlying phellem layer are stimulated to activity and suberin is secreted. This suberin at first seals the crack (Fig. 4 (*a*); Plate 2, Fig. 2) but as further stretching loosens more and more of the phellem, the suberin deposit becomes more widespread (Fig. 4 (*b*)) and a new periderm begins to form, cutting in at an angle from the old one and isolating an area of the cortex which is ultimately shed.

When each successive layer of rhytidome breaks away, or wears away from the stem surface, the layers of the underlying periderm are left as the outermost sealing and protective layer of the stem. The thick-walled lignified cells gradually wear away and leave the suberized layer as the outermost protective layer; this in turn becomes worn and ragged, the cracks again sealing up by suberin secreted from the underlying cells, till a new periderm forms and the process starts again.

The successive periderms thus cut deeper and deeper into the cortex until the whole cortex has been shed. The next-formed periderm then cuts off some of the outer layers of the phloem (Fig. 4 (*b*); Plate 2, Fig. 1).

It is at this stage that the structure of the fully developed bark begins to appear, and differences between the different rhytidome types are first noticed.

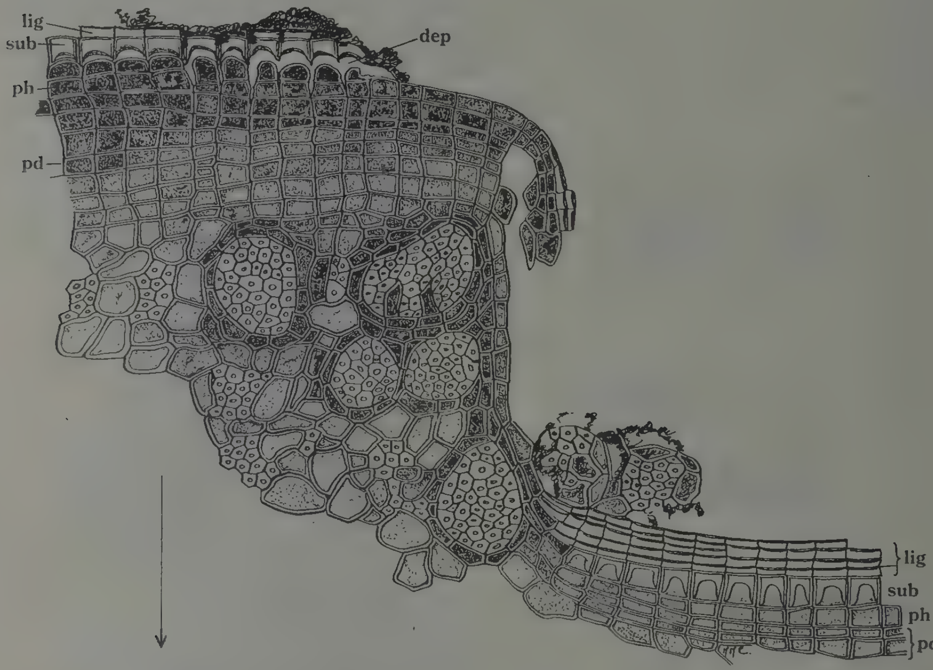


Fig. 5.—*E. regnans.* Old and new periderms. × 225. *ph*, phellogen; *lig*, lignified layer of phellem; *sub*, suberized layer of phellem; *dep*, suberin deposit; *pd*, phelloderm.

V. OLD BARK

(*a*) *General*

The shedding of the bark, which gives the characteristic smooth trunks to so many species of *Eucalyptus* appears to be the retention of the juvenile structure over the whole, or the greater part, of the tree.

The species with a shedding bark usually have very thick-walled cells in the phellem, both in the lignified layer of flattened cells and in the suberized layer. When the rhytidome is shed, these layers provide the outer smooth surface as they do in the young stem.

During the growing season new layers of periderm form here and there in the outer phloem, usually starting just inside the existing periderm and developing as a curving sheath of tissue, cutting off some of the phloem. This layer remains alive for some time, but undergoes changes which result in death, being cut off by the suberized layer of the new periderm from the normal downward flow of food materials, though still in connection with the phloem tissues below. During the growing season and in the heat of the summer the strips of loose bark dry and peel away, usually breaking in the unthickened parenchyma outside the phellem. It is noticeable how many trees strip after a summer spell of unusual heat.

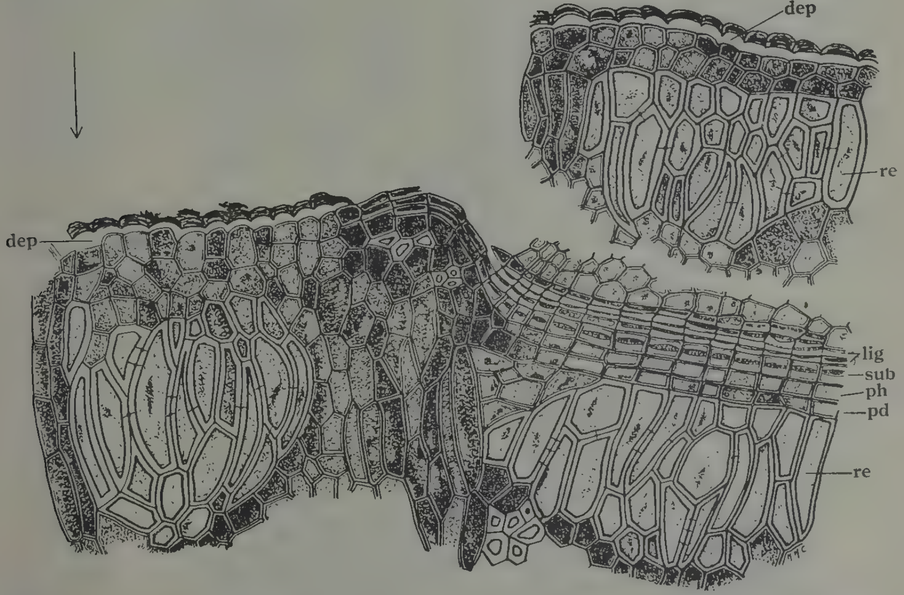


Fig. 6.—*E. rubida.* Old and new periderms, with detached portion of old rhytidome. × 225. The old phellem has been almost worn away, and the suberin deposit (*dep*) is the sealing and protective layer. *dep,* suberin deposit; *lig,* lignified layer of phellem; *sub,* suberized layer of phellem; *ph,* phellogen; *re,* radially elongated phelloderm.

Figure 5 shows part of a cross section through the bark of a young stem of *E. regnans,* with the old periderm just broken away where the new one joins it. The old phellem has been abraded down to the innermost layer, which has become cracked and broken. The cracks have filled up with suberin which was secreted by the living cells below; this forms a waterproof seal and keeps the stem protected till a new periderm has formed. In this specimen the old and new periderms do not meet one another as in that shown in Figure 4 (*b*), but between them there is an area in which most of the phloem parenchyma has become heavily impregnated with tannin and the cell walls are suberized. Such areas are common in the deciduous species at the point of junction of old and new periderms.

The significance of the thickened layers is not yet understood. The thin areas of the phellem cell walls are not, as might be expected, the point at which abscission of the rhytidome takes place. In most material the break takes place outside the thickened layer, the cells of which remain strongly attached to one another.

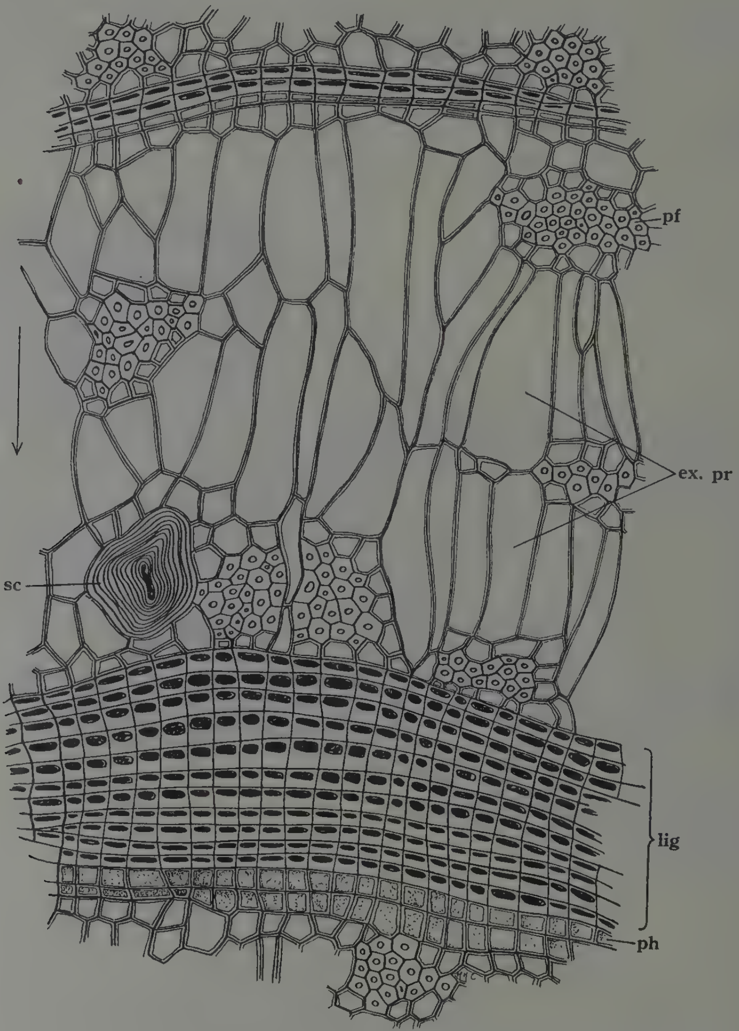


Fig. 7.—*E. macrorrhyncha.* Expanded parenchyma in rhytidome. × 225. *ex. pr,* expanded parenchyma in rhytidome; *pf,* phloem fibres; *sc,* stone-cell; *lig,* lignified layer of phellem; *ph,* phellogen.

Figure 6 shows part of a cross section through the outer phloem of *E. rubida.* From this it can be seen that the break does not take place in the thin-walled part of the flattened lignified phellem, but in the thin-walled tissue outside it.

(*b*) *The Stringybarks*

The very loose bark which gives this group of trees their name is produced by changes occurring in the phloem parenchyma, which lies outside each successive periderm and is in process of becoming rhytidome.

In young stems the tissue cut off by the successive periderms dies, and is shed either as flakes or strips of dried rhytidome, but from about 3-4 years onwards the dead rhytidome remains attached. As each successive periderm forms, the tissues outside it begin to die, as a result of being cut off from their food supply by the suberized layer of the newly formed periderm. As has been observed in the wood when the cells of the sapwood begin to form heartwood (Chattaway 1949, 1952), the first sign of this change is increased activity and growth. Thus all the parenchymatous tissue outside the innermost periderm becomes larger and the resulting loose-celled layers contrast sharply with the more compact phloem within. The phloem parenchyma and ray cells may undergo enormous expansion, often up to many times their previous size, separating the patches of phloem fibres widely and producing a loose, spongy tissue (Fig. 7; Plate 2, Figs. 3, 4, and 5). In the phellem of these species the thickening is usually absent from the suberized layer but, as is shown in *E. macrorrhyncha* in Figure 7, the lignified layer may be of great width. The cells of this layer are strongly cohesive and appear to form a network throughout the rhytidome, holding together the old dry and spongy tissue.

In *E. obliqua* and its allies there is, in addition to rhytidome expansion, an enlargement of the cells of the phelloderm.

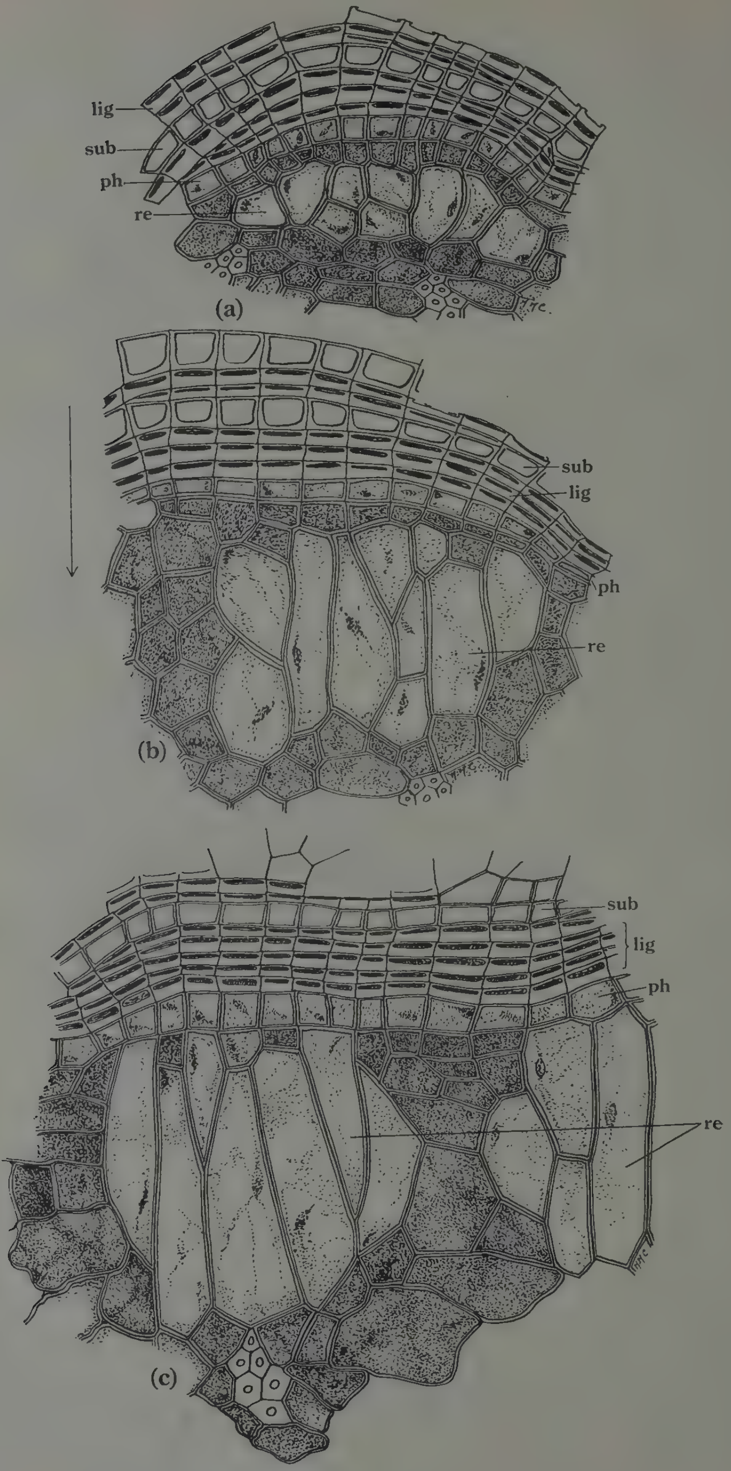
The development of these radially elongated phelloderm cells has been followed in *E. obliqua*. In stems about 3-4 years old the phelloderm cells here and there enlarge a little (Fig. 8 (*a*)) and become noticeable among the smaller tanniniferous cells of the outer phloem and phelloderm. They have conspicuous nuclei.

In larger stems these cells are more frequent and larger (Fig. 8 (*b*), (*c*)), forming tangential bands. Each periderm has a band of such cells in the phelloderm, which appear as successive conspicuous tangential bands on cross sections of old bark. The radially elongated cells do not form a complete sheath around the stem, but are interrupted frequently by masses of more irregular, sometimes even tangentially elongated, cells. They are, however, more regular in the vertical direction, having only infrequent horizontal interruptions.

With the development of each successive phellogen the tissues outside it (which are, until it has finished developing, still part of the living phloem) undergo changes in their metabolism which ultimately cause their death and form the rhytidome.

The thin-walled radially elongated phelloderm appears to form a strongly cohesive layer, and in very old bark only the fibrous patches and the thin-walled radial cells remain as a coherent tissue. The old rhytidome may be retained to a great thickness, wearing away gradually by abrasion (Fig. 9).

Observations on the development of the radially elongated cells from the crown to the base of the tree show that they begin to appear in the small branches soon after the last of the cortex has been cut off, and coincide with


lig
sub
ph
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(a)
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Fig. 8.—For explanation see bottom of page 413.

the first appearance of roughness on the surface of the young stem. They have not been observed in very smooth young twigs.

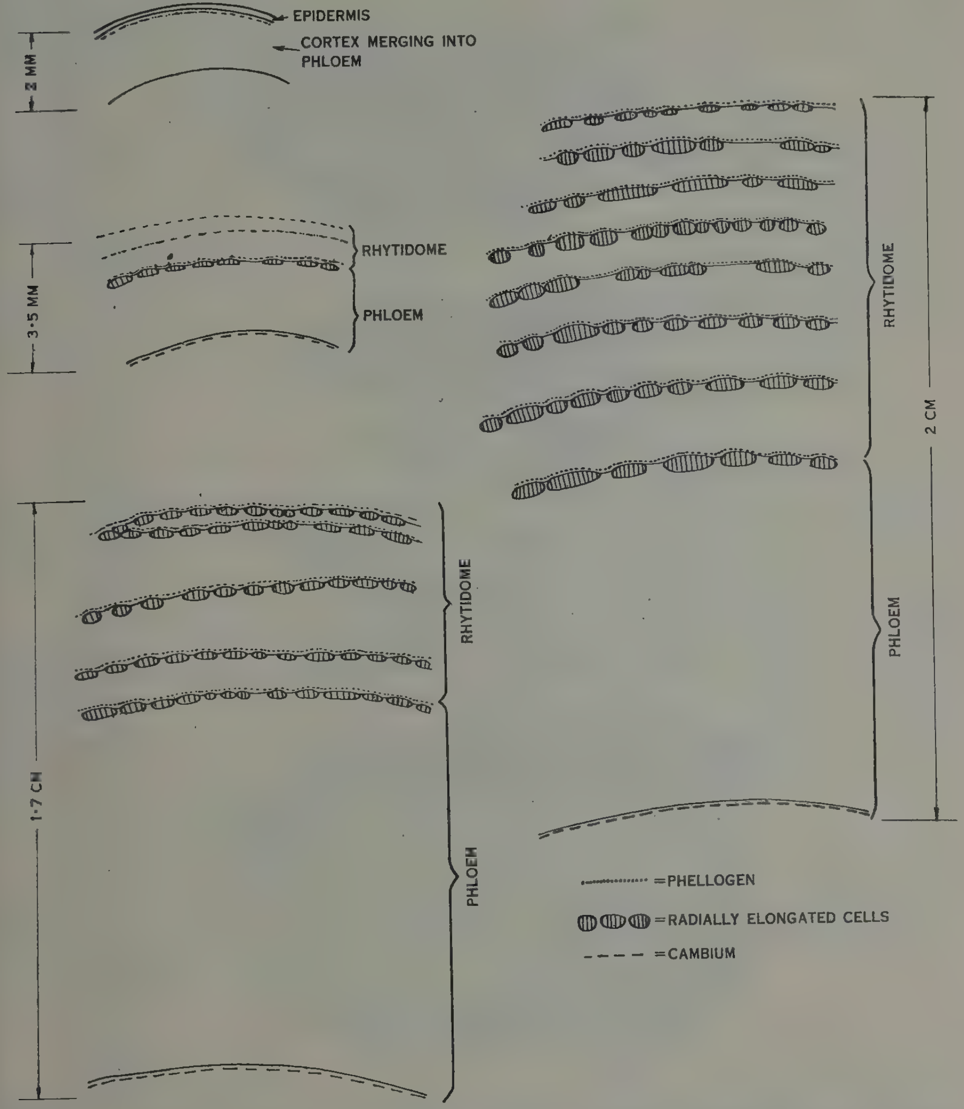
EPIDERMIS
CORTEX MERGING INTO PHLOEM
2 MM
RHYTIDOME
PHLOEM
3·5 MM
RHYTIDOME
PHLOEM
1·7 CM
RHYTIDOME
PHLOEM
2 CM
=PHELLOGEN
=RADIALLY ELONGATED CELLS
=CAMBIUM

Fig. 9.—*E. obliqua.* Diagram to show the development of radially elongated phelloderm cells.

In the semi-deciduous species the full stringybark structure is only developed in the rough basal part of the stem. The transition was studied in *Eucalyptus regnans* from a stand in which all the trees were 6-8 years old. Sections were cut from the base, breast height, and half height of 15 trees.

Fig. 8.—*E. obliqua.* Development of radially elongated cells in the phelloderm of the outer phloem. × 225 approx. *lig,* lignified layer of phellem; *sub,* suberized layer of phellem; *ph,* phellogen; *re,* radially elongated phelloderm.

The formation of the mature rough bark on the base of the tree appears to depend on size rather than on age, for only the larger trees of this even-aged stand had the characteristic rough butts, and only in these were the radially elongated cells developed fully in the smooth stem above the base. In none of the trees examined were the continuous bands of radially elongated cells

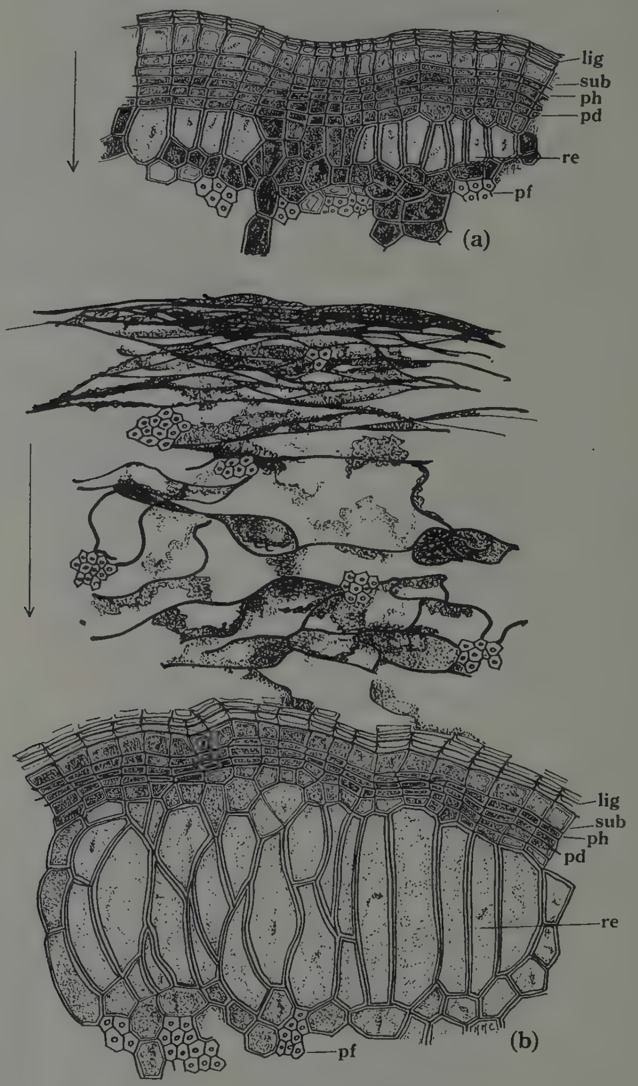

Fig. 10.—*E. regnans.* (*a*) Part of cross section of a block taken from 50 ft up. (*b*) Part of cross section from the butt log of the same tree, showing abraded rhytidome with expanded parenchyma and radially elongated phelloderm. × 225. *lig,* lignified layer of phellem; *sub,* suberized layer of phellem; *ph,* phellogen; *pd,* phelloderm; *re,* radially elongated phelloderm.

formed in the stem at half height and only in two of the largest were they developed at breast height. In about half the trees examined, well-developed radially elongated cells were present in the bark at the base of the log; in the smaller stems they were entirely absent even from the basal discs. But, although the radially elongated cells were not developed to a great height in these young trees, they do occur in the smooth, peeled part of large trees.

These radially elongated phelloderm and expanded parenchyma cells that are so characteristic of the trees with fibrous barks may occur among species from widely different groups.* They are useful features in aiding identification, but it is as yet uncertain how far they can be used in establishing relationships.

The radially elongated phelloderm is a feature of the living tissue of the stem, and can therefore occur in both the deciduous species and those with a persistent rhytidome. It can be seen in *E. rubida* in Figure 6 and has been observed in other smooth-barked species.*

(*c*) *The Boxes and Peppermints*

These trees have a rugose rhytidome, which is semi-fibrous and persistent. It is formed by a succession of closely spaced, often anastomosing periderms, which may be many cells wide and are usually without any marked thickening of either the suberized or lignified layers of the phellem.

The expanding girth of the stem causes an excessive development of the parenchyma in these barks, stimulating the phloem parenchyma to localized growth. The mature bark consists of alternating wedges of secondary phloem and thin-walled parenchyma (Plate 3, Figs. 1 and 2). The phloem wedges taper towards the periphery of the stem, the parenchyma wedges towards the cambium. The wedges may cross several periderms and often form the points of weakness at which the fine fissures that are so common in these barks develop (Plate 3, Fig. 1).

Parenchyma wedges occur in many other species to a lesser degree. This is an understandable way of increasing the circumference of the phloem as the tree grows. It reaches its greatest development, however, in the boxes, peppermints, and gums (Plate 3, Figs. 1-3).

(*d*) *The Blue Gums and Manna Gums*

In many of the gums the parenchyma wedges contain numerous large oil glands. They are a secondary development in the phloem, occurring only in the tissue which forms as a result of tangential growth. Though they can be found deep into the phloem they have always developed in tissue which has resumed active growth, and never in the ordinary parenchyma of the inner phloem. The localization of the oil glands in the parenchyma wedges is seen clearly in Plate 3, Figures 2 and 3, and Plate 4, Figure 1. Wherever the oil glands occur the cells of the parenchyma have enlarged and begun to form wedges; there are none in the small-celled parenchyma of the rest of the phloem.

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* See list of features in Appendix.

(*e*) *The Red Gums and Snappy Gums*

The red gums, as a group, usually have small wedges of parenchyma without oil glands; some of them have radially elongated cells in the phelloderm, and many of them have very wide, spongy phellem. This results from the development of a wide phellem without much thickening. The suberized cells are, as in the other groups, almost isodiametric and have thin suberized walls, but no inner thickening is laid down in these species and the cells remain thin-walled all their lives. Alternating with the suberized layer are the usual rows of lignified cells, but these too remain unthickened and may be extended radially (Fig. 11). Plate 4, Figure 2, and Figure 11 show the alternating layers of thin-walled phellem in *E. parramattensis*. When sections are stained in Sudan

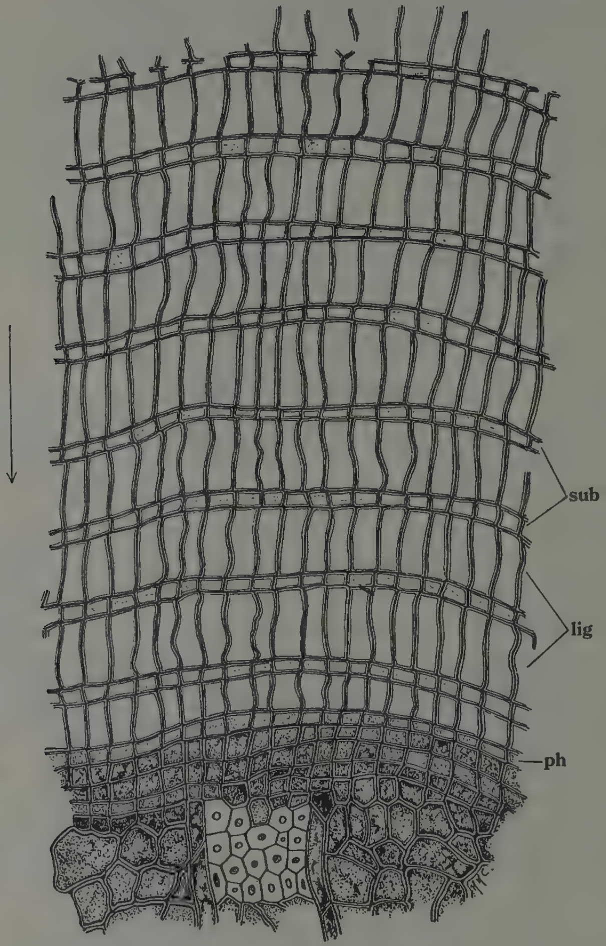

Fig. 11.—*E. parramattensis*. Cross section of phellem, showing the narrow suberized and wide, unthickened lignified cells. × 225. *sub*, suberized layer; *lig*, lignified layer of phellem; *ph*, phellogen.

IV the colour contrast between the different layers is most marked, the suberized layers (showing darker in Plate 4, Fig. 2) are red and the lignified cells are uncoloured. Some of the species in this group have radially elongated cells in the phelloderm and most of them have groups of fibres which have a greater diameter than the rest. The two latter features are also characteristics of the

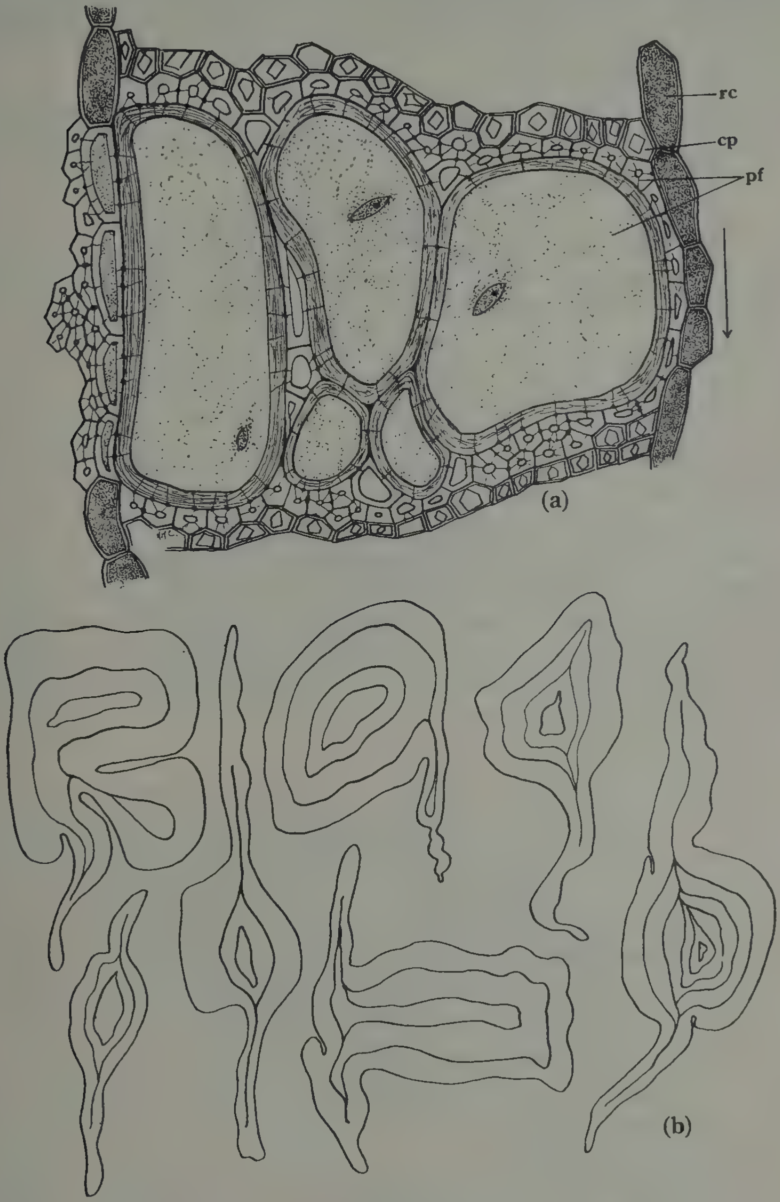

Fig. 12.—*E. gummifera.* (*a*) Expanded fibres in the region of the cambium (cross section × 225). (*b*) Macerated fibres. × 160. *rc,* ray cells; *cp,* crystalliferous parenchyma; *pf,* phloem fibres.

snappy gums, *E. micrantha, E. haemastoma,* and *E. rossii.* In these species the smooth stems are abraded and peeled down to the innermost periderm, the cells of the phelloderm are radially elongated (Plate 4, Fig. 3), and patches of fibres with greater cross-sectional diameter occur scattered among the rest of the phloem fibres (Plate 4, Fig. 4).

The smooth-barked mallees are usually without many distinctive features in the bark; sometimes parenchyma wedges develop in the bark of the larger stems.

(*f*) *The Bloodwoods*

The epidermis and early stages of periderm formation in the bloodwoods are similar to those observed in other species of eucalypt, but there are peculiarities in the structure of the phloem that have so far only been found in this group of species.

The group divides into two sections, to one of which belong the rough-barked species and to the other the smooth and partially deciduous species.

The phloem of the rough-barked species is characterized by the presence of enormously expanded fibres. These are formed immediately the fibres are cut off from the cambium, and the expansion must be completed, as in the vessels of the wood, before any secondary thickening is laid down. Figure 12 (*a*) shows groups of expanded fibres in the immediate vicinity of the cambium; the fibres have expanded to their full amount and secondary thickening has started. The nuclei and protoplasm are often still visible. The thickening of the walls must take place very quickly, for only the last-formed fibres are still relatively thin-walled. Figure 12 (*b*) shows the outlines of some of these irregularly shaped fibres.

In twigs and very small stems the structure is similar to that observed in other species of *Eucalyptus* except for some of the ray cells, which are very much thickened where they pass through a group of fibres (Fig. 13 (*a*)). This thickening is equally well developed in older stems but is masked by the expansion of the fibres. The transition from normal fibres to the expanded ones is gradual, at first a few large fibres occur in some patches of fibres scattered through the phloem. They first appear when the successive periderms have cut off most of the cortex and are beginning to develop into the phloem (Fig. 13 (*b, c*)).

In some species the later development of the stem is marked by the formation of a very spongy rhytidome, very similar to that observed in *E. macrorrhyncha.* As in that species, as each new periderm is formed the parenchyma of the newly cut off rhytidome undergoes enormous expansion. In extreme cases, in *E. abbreviata* and *E. polycarpa,* a very large number of periderms develop and the fibre bundles become separated from one another by the expanded parenchyma. Thirty-four such periderms were observed in the very wide rhytidome of *E. abbreviata.*

This type of structure has been observed in all the rough-barked species except *E. jacobsiana* and *E. ficifolia*; the fibre expansion in *E. eximia* (one sample only) was much less than in the other species examined.

The deciduous species have, however, an entirely different type of phloem structure. The fibres have a normal, small diameter, even in mature material, and appear in cross sections of the inner part of the phloem as broken tangential bands (Fig. 14; Plate 5, Fig. 1) surrounded by crystalliferous cells and separated by several rows of parenchyma. As the stem increases in diameter this parenchyma expands (usually tangentially but occasionally radially) and in

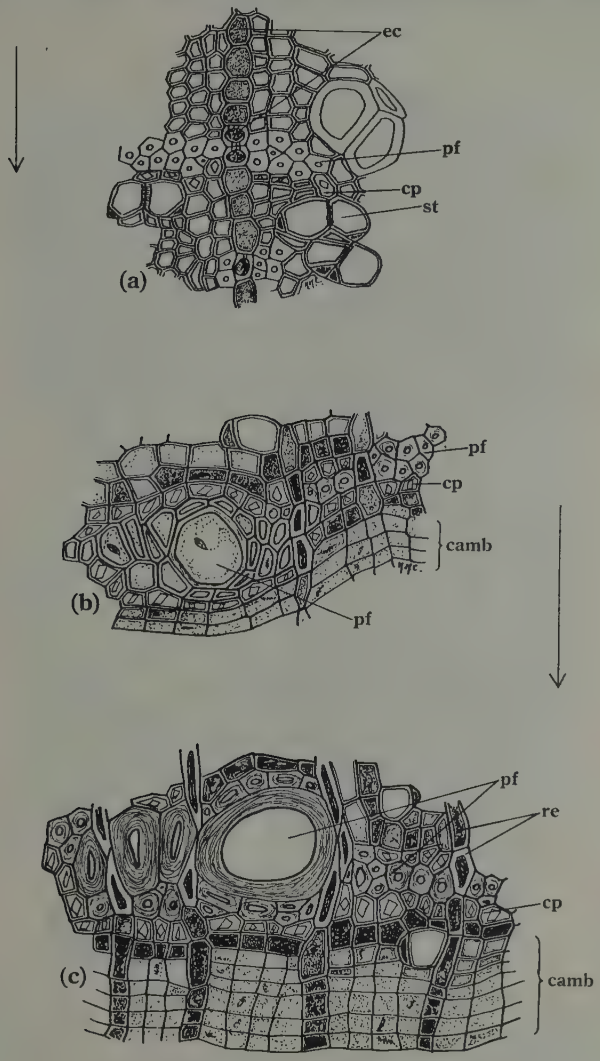

Fig. 13.—*E. gummifera.* (*a*) Cross section of very young stem, showing thick-walled ray cells in the fibre patches. (*b*) and (*c*) Stages in the development of enlarged fibres. All × 225. *rc,* ray cells; *pf,* phloem fibres; *cp,* crystalliferous parenchyma; *st,* sieve tubes; *camb,* cambium.

some species, the cells become sclerosed (Fig. 15). Although the cells are parenchymatous in origin they communicate with one another by means of *bordered* pits. The final stage of development, just inside the periderm, produces a very irregular tissue, brittle and gritty to feel, in which the meanderings of the tannin-filled rays, which have been deflected from their normal courses by expansion of the surrounding tissue, are very noticeable (Fig. 15; Plate 5, Figs. 2 and 3).

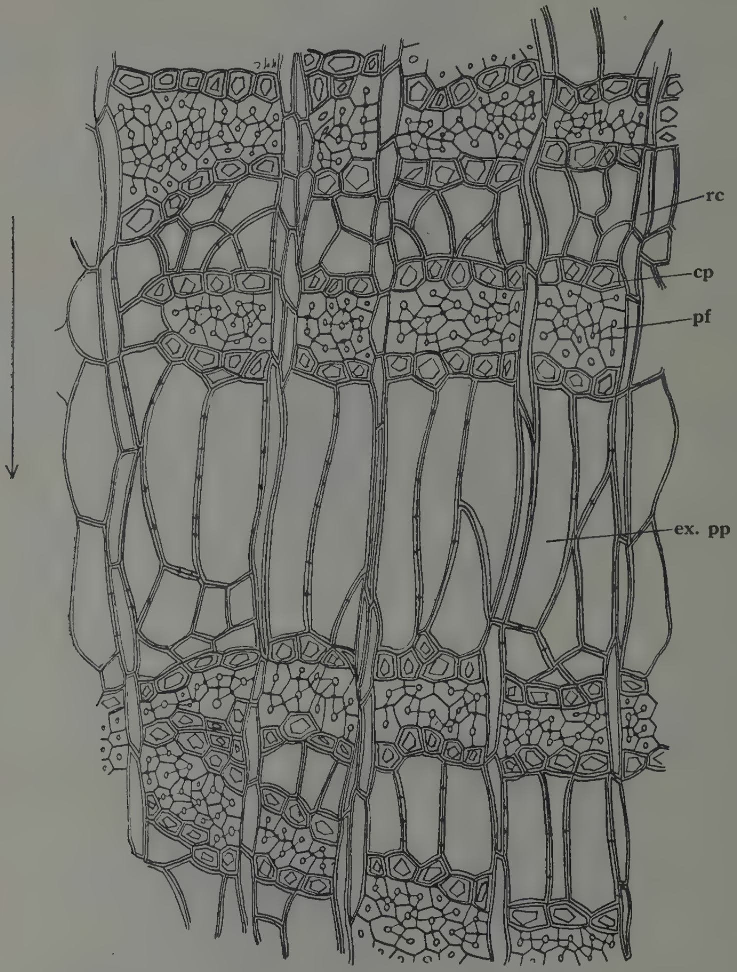

Fig. 14.—*E. maculata.* Cross section of outer phloem, to show radially expanded parenchyma. × 225. *rc,* ray cells; *pf,* phloem fibres; *cp,* crystalliferous parenchyma; *ex. pp,* expanded phloem parenchyma.

(g) *The Ironbarks*

The extremely hard, black, furrowed, and persistent rhytidome of *Eucalyptus sideroxylon* and the softer but still very wide, ridged, and persistent bark of some of the other species in this group appear to be quite different in development and structure from the barks already described. The structure of the phloem and cortex of twigs is similar to that observed in other eucalypts, but after the cortex has been cut off the succession of spaced periderms which, in other species, cut off comparatively unchanged segments of cortex or phloem,

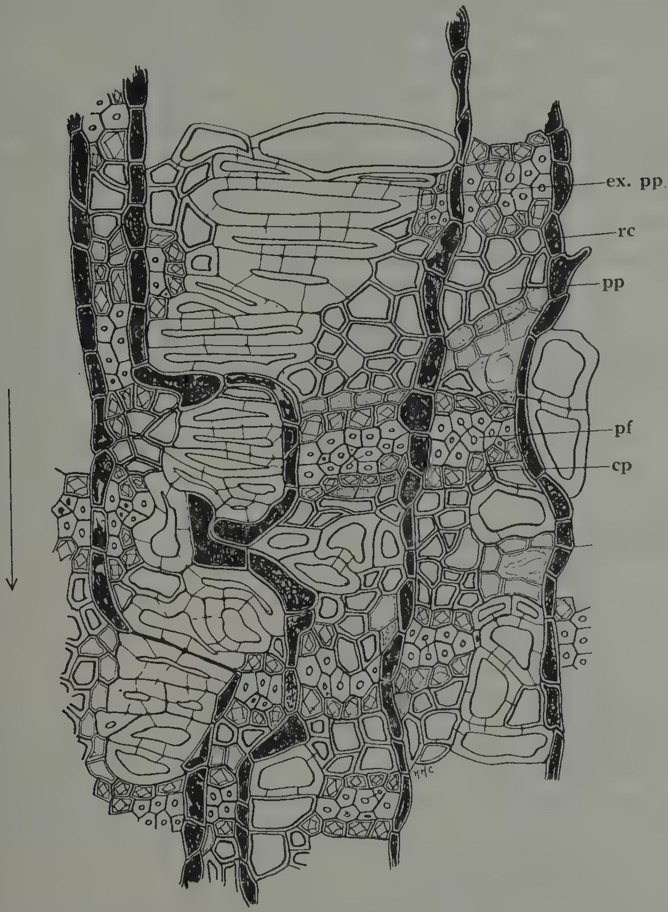

Fig. 15.—*E. aspera.* Cross section of outer phloem, to show tangentially expanded and thickened parenchyma and distortion of ray direction. × 225. *ex. pp,* expanded phloem parenchyma; *rc,* ray cells; *pp,* phloem parenchyma; *pf,* phloem fibres; *cp,* crystalliferous parenchyma.

is replaced by a meristematic development of almost all the phloem parenchyma. Many of the narrow bands of parenchyma divide by tangential walls to form wider bands (Plate 6, Fig. 1) which continue to grow and divide until a very wide spongy tissue has been formed, in which the fibre bundles are separated from one another by masses of very thin-walled tissue (Plate 5, Fig. 4). This tissue is very variable and adjacent meristems may produce quite different types of phellem. The resultant rhytidome may consist of a wide mass of thin-walled suberized tissue which may contain localized areas of dead phloem in which the parenchyma has not become meristematic, of areas in which bands of thick-walled lignified phellem cells have been formed, and of areas of phellem in which thin-walled suberized and lignified cell layers alternate as in the phellem of the red gums. In almost all the the ironbarks the rhytidome contains kino pockets. In their early stages of development these appear as areas of enlarged parenchyma cells (Plate 6, Fig. 4) which grow and divide to produce an ever-enlarging area of tissue with large cells and thin walls. Gradually this tissue disintegrates, absorbing adjacent fibre masses and leaving a cavity filled with liquid kino. The smaller kino pockets are usually surrounded by a periderm which isolates them from the neighbouring tissue; it consists of suberized and thick-walled lignified phellem towards the cavity and a few rows of phelloderm towards the phloem (Plate 6, Fig. 5). In old rhytidome these kino pockets have often burst the confines of the periderm and extend through a considerable area of the rhytidome.

The furrows that are such a feature of this group are the direct result of this wide rhytidome; the expanding girth of the stem causes small cracks which, being areas of weakened tissue, deepen into furrows in older stems.

In some ironbarks the whole rhytidome becomes heavily impregnated with liquid kino which hardens and darkens on exposure to the air, producing the hard rhytidome from which the group takes its name. The rhytidome may become several inches in thickness.

VI. DISCUSSION

(*a*) *General*

The functions of the different layers of the phellem are somewhat obscure. The suberized layer is considered to be responsible for the death of the cells outside it, but the death of these cells is a slow process and during the metabolic changes that occur while the cells are dying there is certainly at some time a stimulus to increased growth, so that the cells may enlarge to many times their original size after the formation of the periderm.

The thickening of the phellem cells, which, in many species, is laid down so that thin places are left on the radial walls, suggests that the phellem layers are the ones in which the abscission of the rhytidome takes place. Actually this is not so, and in every section of smooth-barked species in which the abscission of the rhytidome could be observed, the break took place in the layers of thinner-walled tissue outside the phellem. This is clearly shown in Figure 6. It appears that these strongly thickened cells are directly connected not with the abscission of the rhytidome but with the protection of the underlying layer of living phloem. They adhere tightly to one another, forming a strong, heavily thickened sheath outside the phloem. They have no intercellular spaces and as they wear away and the phellem layer becomes cracked and ragged, their protective function is taken over by the deposits of suberin, the secretion of which appears to be the reaction of the underlying cell to exposure to air. They are present in all the species with deciduous rhytidome and occur only sporadically in most of the species with persistent rhytidome, except the stringybarks in which they are sometimes very common (Fig. 7).

The suberized layer of the phellem is thickened only in deciduous species, in the smooth parts of semi-deciduous species, and in the young, smooth stems of the rough-barked species. It is probable therefore that this inner layer of thickening materially assists the shedding of the rhytidome through causing unequal tensions in this layer, even though the phellem layer is not where the break actually takes place.

A peculiar feature of the phloem of many *Eucalyptus* species is the occurrence of parenchyma cells which communicate with one another, and with adjacent cells through bordered pits. These pits are often very difficult to see in young material in which the cell walls are very thin, but they sometimes become a very conspicuous feature of the thick-walled stone cells which develop as the outer phloem ages. They have been seen in the radially elongated cells of the phelloderm (Fig. 6) and in the expanded phloem parenchyma (Figs. 14, 15), but they vary very much in size and distinctness from species to species. Their function is obscure, especially in the radially elongated phelloderm cells, which are formed in the oldest part of the phloem, in which conduction has almost certainly ceased.

(*b*) *Classification*

For many years macroscopic features of the bark have been used as a basis of classification of the gums. These may now be supplemented by microscopic features. It appears, however, unlikely that the structure of the bark will ever be used in minute detail for the purpose of classification, but certain features of the phloem and rhytidome may prove useful as additional features to aid in the identification of species and elucidation of relationships.

As the material available for examination was unevenly distributed through the different groups no attempt is made to discuss fully the bearing of the bark structure upon classification, except in well-represented groups where distinct alliances or discrepancies can be traced.

In the bloodwoods (*Corymbosae* and *Corymbosae-peltatae*), for example, the rough- and smooth-barked species are quite as distinct from one another in detail as they are in gross structure, and there is a distinct similarity between the smooth-barked species and some of the species of *Angophora*.

Among the rough-barked species three were somewhat aberrant, *E. jacobsiana*, of which only one sample was available, *E. ficifolia*, and *E. calophylla*. *E. ficifolia* was without the large, expanded fibres so characteristic of all the other rough-barked species, and material of *E. calophylla* contained some samples of typical structure and some without the enlarged fibres. In view of the constant interbreeding of ornamental trees of the two red-flowering species this is hardly surprising in cultivated trees; hybridization is also reported from the natural habitat of the species.

The formation of wedges of parenchymatous tissue as a means of accommodating the outer phloem to the increasing girth of the stem is a common feature, but in the gums (*Subexsertae*, *Globulares*, *Viminales*, and *Argophyllae*) oil glands develop throughout this secondary tissue and form a very conspicuous feature of the outer phloem. In the *Globulares, E. goniocalyx, E. globulus,* and *E. bicostata* appear to differ from the others; some specimens are without the oil glands that form so conspicuous a feature of these groups.

In the *Diversaeformes, E. diversifolia* appears to have parenchyma wedges and oil glands in common with the four preceding groups, whereas the only other species examined, *E. todtiana,* is without these features but has the expanded rhytidome parenchyma that is characteristic of the stringybarks.

The loose bark of the white mahoganies and stringybarks is formed by the expansion of the phloem parenchyma after the development of the periderm. The ashes (*Fraxinales*) have, in addition to this feature, bands of rapidly elongated phelloderm which are often visible even with a hand lens. This feature is also well developed in *E. obliqua* and *E. regnans.* On both the macroscopic and microscopic structure of the bark these two species appear to have more in common with the ashes than with the stringybarks.

E. pauciflora differs from the other snow gums (*Longitudinales*) in the presence of radially elongated phelloderm cells; the other members of this group and the peppermints (*Piperitales*) have few distinctive features; though some of them have quite conspicuous parenchyma wedges, these are without any oil glands.

The snappy gums examined (three species of *Psathyroxyla*) form a compact and homogeneous group. They have occasional groups of phloem fibres with wide cross-sectional diameters which, though much less marked than those of the rough-barked bloodwoods, are a very conspicuous feature of cross sections. They also have radially elongated phelloderm cells.

The boxes (*Buxeales* and *Sub-buxeales*) form a group in which there are few distinctive features; the species examined showed many successive rather convoluted and anastomosing periderms, and in some of them kino pockets were frequent in the outer phloem.

The bark of the ironbarks (*Siderophloiae*) has already been fully described. With the exception of *E. leucoxylon,* they form a homogeneous group with a peculiar type of phellogen development and with frequent and extensive kino pockets developing in the outer phloem.

Among the *Exsertae, E. camaldulensis,* and *E. dealbata* differ from the others in the occasional presence of radially elongated phelloderm. In *E. camaldulensis* this feature has so far been well developed only in material collected along the Murray River.

The mahoganies (*Transversae*) form another heterogeneous group in regard to bark structure; most of the species examined have rather indeterminate barks, with small parenchyma wedges and slightly expanded phellem cells. But *E. saligna, E. deanei, E. botryoides,* and *E. longifolia* have radially elongated phelloderm cells, and *E. botryoides, E. kirtoniana,* and *E. pellita* have expanded parenchyma in the rhytidome.

This brief review of the classification is of necessity generalized and many groups are omitted. It may, however, serve a useful purpose by drawing attention to the homogeneity of some of the groups which Blakely based on another structure, and to discrepancies in others, and is intended to show how details of bark structure can be called in to the aid of the systematic botanist. In the meantime more material of the aberrant species is being collected and a fuller discussion of this aspect of the work will form the subject of a subsequent paper.

(*c*) *Identification*

Details of bark structure have already proved of use in identification of species which are very similar in other respects and it is likely that, as the anatomy of more barks is known, this aspect of the work can be extended.

E. viminalis and *E. rubida,* two deciduous species, are very difficult to distinguish unless seedlings with juvenile foliage are available. But *E. rubida* (Fig. 6) has radially elongated phelloderm cells, whereas these cells are absent from *E. viminalis*. *E. dalrympleana* can be separated from *E. viminalis* by similar characters.

The bark characters are also likely to be of great use in the elucidation of hybrids. This aspect of the work will also be treated in a subsequent paper.

VII. ACKNOWLEDGMENTS

The author would like to acknowledge her indebtedness to Miss Patricia Maloney, to whose lot fell the onerous task of preparing the many hundreds of slides used in this investigation, and to all who have provided material.

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EXPLANATION OF PLATES 1-6

PLATE 1

Fig. 1.—*E. obliqua.* Cross section of young stem. × 33.

Fig. 2.—*E. obliqua.* Cross section of young stem; outer cortex, epidermis, and oil glands. × 135.

Fig. 3.—*E. obliqua.* Cross section of slightly older stem; stretched cortical parenchyma. × 200.

Fig. 4.—*E. obliqua.* Cross section of outer cortex; details of periderm. × 150.

Fig. 5.—*E. regnans.* Cross section of outer cortex; details of phellem and suberin deposits. × 188. As above; *dep*, suberin deposits.

PLATE 2

Fig. 1.—*E. australiana.* Cross section of outer phloem; young periderm developing inside old one. *dep,* suberin deposits sealing cracks in old phellem. × 140.

Fig. 2.—*E. australiana.* Cross section of outer phloem; *dep,* suberin deposit under crack in suberized layer of phellem. × 700.

Fig. 3.—*E. macrorrhyncha.* Cross section of outer edge of phloem and series of periderms; expanded parenchyma of rhytidome. × 17.

Fig. 4.—*E. macrorrhyncha.* Part of the above enlarged. × 48.

Fig. 5.—*E. muelleriana.* Cross section of outer phloem and inner rhytidome. × 29.

PLATE 3

Fig. 1.—*E. melliodora.* Cross section of outer phloem; parenchyma wedges cracked in rhytidome. × 25.

Fig. 2.—*E. ovata.* Cross section of outer phloem and inner rhytidome; parenchyma wedges with oil glands. × 21.

Fig. 3.—*E. macarthuri.* Tangential section of inner phloem; parenchyma wedges with oil glands. × 51.

PLATE 4

Fig. 1.—*E. elaeophora.* Cross section of part of parenchyma wedge with oil glands. × 55.

Fig. 2.—*E. parramattensis.* Cross section of phellem. *a,* suberized layer; *b,* thin-walled lignified layer. × 62.

Fig. 3.—*E. rossii.* Cross section of outer phloem; suberized and lignified cells of phellem and radially elongated phelloderm. × 88.

Fig. 4.—*E. micrantha.* Cross section of phloem. *a,* patch of fibres with enlarged cross section. × 88.

PLATE 5

Fig. 1.—*E. papuana.* Cross section of phloem; wide phelloderm and tangential bands of fibres and parenchyma. × 11.5.

Fig. 2.—*E. maculata.* Cross section of outer phloem; wide phelloderm and enlarged and sclerosed parenchyma cells. The tannin-filled rays take an irregular course around the parenchyma cells. × 70.

Fig. 3.—*E. citriodora.* Cross section of outer phloem; wide phelloderm and irregularly expanded parenchyma. × 102.

Fig. 4.—*E. drepanophylla.* Cross section of wide, spongy rhytidome. × 12.5.

PLATE 6

Fig. 1.—*E. drepanophylla.* Cross section of outer phloem; periderm formation in phloem parenchyma. × 69.

Fig. 2.—*E. drepanophylla.* Cross section of rhytidome, spongy tissue resulting from growth of a series of periderms. × 27.

Fig. 3.—*E. sideroxylon.* Cross section of phloem and rhytidome. × 14.5.

Fig. 4.—*E. sideroxylon.* Cross section of phloem; early stage in the formation of a kino pocket. × 65.

Fig. 5.—*E. sideroxylon.* Cross section of phloem; later stage of the same. × 170.

APPENDIX 1

DETAILS OF OBSERVATIONS

Number in Blakely (1934)	Species	Rhytidome Type*	Expanded Parenchyma in Rhytidome	Wide Phellem	Fibres with Enlarged Cross Section	Conspicuous Parenchyma Wedges	Oil Glands in Wedges	Expanded Parenchyma in Phloem	Radially Elongated Phelloderm	Kino Pockets
	I. *Eudesmieae*									
7	*tetrodonta* F. Muell. (3)	P	(+)			(+)	+			
12	*baileyana* F. Muell. (1)	P								+
	II. *Miniatae*									
13	*phoenicea* F. Muell. (1)	P			+					
14	*miniata* A. Cunn. (1)	P	+		+					
	IV. *Corymbosae*									
17	*papuana* F. Muell. (2)	S						+		
19	*clavigera* A. Cunn. (1)	S						+		
21	*aspera* F. Muell. (1)	D						+		
22	*setosa* Schauer (1)	P	+		+					
23	*ferruginea* Schauer (2)	S	(+)		+					
23*a*	*abbreviata* Blakely & Jacobs (1)	P	+		+					
26	*dichromophloia* F. Muell. (2)	P	+		+					
27	*terminalis* F. Muell. (1)	P	(+)		+					
28	*abergiana* F. Muell. (3)	P	+		+					
31	*ptychocarpa* F. Muell. (1)	P	(+)		+					
	V. *Corymbosae-peltatae*									
32	*calophylla* R. Br. (8)	P	+		(+)°					
36	*ficifolia* F. Muell. (6)	P	+							
41	*polycarpa* F. Muell. (4)	P	(+)		+					
45	*gummifera* (Gaertn) Hochr. (6)	P	(+)		+					
46	*intermedia* R. T. Baker (2)	P	(+)		+					
50	*eximia* Schauer (1)	P	(+)		+					
52*a*	*jacobsiana* Blakely (1)	P	No distinctive features observed							
53	*citriodora* Hook. (4)	D						+		
54	*maculata* Hook. (3)	D						+		
	VI. *Transversae*									
57	*diversicolor* F. Muell. (2)	D		+		(+)				
58	*grandis* Maiden (6)	D				(+)			(+)°	
60	*saligna* Smith (6)	D							+	
62	*deanei* Maiden (1)	D							+	
64	*botryoides* Smith (5)	P	+						+	
71	*kirtoniana* F. Muell. (1)	P	+							

*P = persistent rhytidome; D = deciduous rhytidome; S = semi-deciduous rhytidome.

+° Indicates conflicting evidence for the feature.

(+) Indicates that a feature is less conspicuous than usual or somewhat sporadic in its occurrence.

Appendix 1 (*Continued*)

Number in Blakely (1934)	Species	Rhytidome Type*	Expanded Parenchyma in Rhytidome	Wide Phellem	Fibres with Enlarged Cross Section	Conspicuous Parenchyma Wedges	Oil Glands in Wedges	Expanded Parenchyma in Phloem	Radially Elongated Phelloderm	Kino Pockets
	VI. *Transversae* (Continued)									
73	*pellita* F. Muell. (2)	P	+							
78	*punctata* DC. (6)	S		+		+			+°	
80	*canaliculata* Maiden (2)	D		+					+°	
81	*longifolia* Link & Otto. (7)	S		+					+	
	VII. *Obliquae*									
91	*stricklandi* Maiden (2)	S				+				
92	*griffithsii* Maiden (1)	S	No distinctive features observed							
	VIII. *Cornutae*									
97	*lehmanni* Preiss (3)	D	No distinctive features observed							
98	*gomphocephala* A. DC. (2)	P		+				+		
99	*platypus* Hook. (2)	D				(+)	+			
110	*occidentalis* Endl. (3)	S				(+)				
112	*astringens* Maiden (2)	D						+		
	X. *Microcorythae*									
121	*cladocalyx* F. Muell. (6)	D		(+)		+				
	XI. *Dumosae*									
134	*dundasi* Maiden (1)	S	No distinctive features observed							
136	*incrassata* Labill. (1)	D				(+)				
143	*brachycorys* Blakely (1)	P	No distinctive features observed							
144	*brachycalyx* Blakely (1)	S				(+)				
146	*pileata* Blakely (1)	D				(+)				
157	*le souefi* Maiden (1)	S				(+)				
159	*torquata* Luehmann (3)	P		(+)		(+)				
	XIII. *Decurvae*									
168	*falcata* Turcz. (2)	D				+				
	XV. *Exsertae*									
178	*tereticornis* Smith (6)	D		+		+				
184	*amplifolia* Naudin (1)	D		(+)	(+)	+				
186	*blakelyi* Maiden (12)	D				(+)			(+)°	
189	*dealbata* A. Cunn. (1)	S							(+)°	
190	*dwyeri* Maiden & Blakely (1)	D	No distinctive features observed							

*P = persistent rhytidome; D = deciduous rhytidome; S = semi-deciduous rhytidome.
+° Indicates conflicting evidence for the feature.
(+) Indicates that a feature is less conspicuous than usual or somewhat sporadic in its occurrence.

APPENDIX 1 (*Continued*)

Number in Blakely (1934)	Species	Rhytidome Type*	Expanded Parenchyma in Rhytidome	Wide Phellem	Fibres with Enlarged Cross Section	Conspicuous Parenchyma Wedges	Oil Glands in Wedges	Expanded Parenchyma in Phloem	Radially Elongated Phelloderm	Kino Pockets
	XV. *Exsertae* (Continued)									
192	*parramattensis* Hall (1)	D		+	(+)	(+)				
194	*seeana* Maiden (5)	D		+	(+)				(+)	
196	*bancrofti* Maiden (1)	D		+	(+)					
197	*camaldulensis* Dehn. (24)	D			(+)				(+)°	
204	*rudis* Endl. (3)	P						(+)		
	XVI. *Subexsertae*									
208	*platyphylla* F. Muell. (1)	D	No distinctive features observed							
210	*ovata* Labill. (9)	S				+	+			
212	*camphora* R. T. Baker (1)	S				+	+			
215	*aggregata* Deane & Maiden (2)	P				+	+			
	XVII. *Microcarpae*									
220	*maculosa* R. T. Baker (5)	D				+	+		+	
	XVIII. *Globulares*									
223	*dunnii* Maiden (1)	D				+	+			
224	*angophoroides* R. T. Baker (1)	P				+	+			
225	*stuartiana* F. Muell. (2)	P				+	+			
229	*elaeophora* F. Muell. (16)	P				+	+			
230	*cordieri* Trabut (2)	P				+	+			
235	*rubida* Deane & Maiden (7)	D				+	+		+	
236	*dalrympleana* Maiden (3)	D				+	+		+	
248	*globulus* Labill. (11)	D				+	+°			
250	*bicostata* Maiden Blakely & Simmonds (6)	S				+	+°			
261	*maideni* F. Muell. (2)	D				+	+			
262	*goniocalyx* F. Muell. (28)	S				+	+°		+°	
263	*nitens* Maiden (1)	S				+	+			
	XIX. *Semiunicolores*									
265	*neglecta* Maiden (1)	P	No distinctive features observed							
	XX. *Viminales*									
271	*badjensis* de Beuzeville & Welch (1)	S		+		+	+			
272	*quadrangulata* Deane & Maiden (1)	S				+				
273	*macarthuri* Deane & Maiden (2)	S				+	+			

*P = persistent rhytidome; D = deciduous rhytidome; S = semi-deciduous rhytidome.

+° Indicates conflicting evidence for the feature.

(+) Indicates that a feature is less conspicuous than usual or somewhat sporadic in its occurrence.

Appendix 1 (*Continued*)

Number in Blakely (1934)	Species	Rhytidome Type*	Expanded Parenchyma in Rhytidome	Wide Phellem	Fibres with Enlarged Cross Section	Conspicuous Parenchyma Wedges	Oil Glands in Wedges	Expanded Parenchyma in Phloem	Radially Elongated Phelloderm	Kino Pockets
	XX. *Viminales* (Continued)									
274	*smithii* R. T. Baker (1)	S				+	+			
275	*benthami* Maiden & Cambage (1)	S				+	+			
277	*viminalis* Labill. (14)	S				+	+			+?
280	*huberiana* Naudin (1)	S				+	+			
	XXI. *Argyrophyllae*									
283	*cinerea* F. Muell. (4)	P	+			+	+			
284	*cephalocarpa* Blakely (1)	P	+			+	+			
	XXII. *Paniculatae*									
288	*gamophylla* F. Muell. (1)	P				(+)				
	XXIII. *Diversiformae*									
297	*diversifolia* Bonpl. (1)	D				+				
298	*todtiana* F. Muell. (1)	P	+							
	XXIV. *Occidentales*									
304	*marginata* Smith (3)	P	+			(+)				
	XXVI. *Pseudo-stringybarks*									
306	*pilularis* Smith (5)	P	+°						+	
308	*muelleriana* Howitt (2)	P	+							
	XXVII. *White Mahoganies*									
311	*umbra* R. T. Baker (1)	P	+							
313	*triantha* Link (1)	P	(+)							
	XXVIII. *Steatoxylon* (*tallow-woods*)									
314	*microcorys* F. Muell. (1)	P	+							
	XXIX. *Pachyphloiae* (*stringy-barks*)									
318	*wilkinsoniana* R. T. Baker (1)	P	No distinctive features observed							
331	*macrorrhyncha* F. Muell. (5)	P	+							
336	*blaxlandi* Maiden & Cambage (1)	P	+							
340	*capitellata* Smith (2)	P	+							

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Appendix 1 (*Continued*)

Number in Blakely (1934)	Species	Rhytidome Type*	Expanded Parenchyma in Rhytidome	Wide Phellem	Fibres with Enlarged Cross Section	Conspicuous Parenchyma Wedges	Oil Glands in Wedges	Expanded Parenchyma in Phloem	Radially Elongated Phelloderm	Kino Pockets
	XXIX. *Pachyphloiae* (*stringy-barks*) (Continued)									
345	*agglomerata* Maiden (1)	P	+			+				
349	*scabra* Dum-Cours (3)	P	+							
362	*obliqua* L'Hérit. (6)	P	(+)			(+)			+	
368	*fastigata* Deane & Maiden (3)	P	+			+			+	
369	*regnans* F. Muell. (28)	S	+						+	
	XXX. *Fraxinales*									
370	*gigantea* Hook. f. (6)	S	+			(+)			+	
371	*sieberiana* F. Muell. (5)	S	+	+		+				+°
373	*consideniana* Maiden (2)	S				+			(+)	
377	*planchoniana* F. Muell. (1)	P			(+)				(+)	
380	*oreades* R. T. Baker (1)	S		+		+				
	XXXI. *Longitudinales* (*snow gums*)									
392	*vitrea* R. T. Baker (5)	P		(+)°	(+)	+				
394	*pauciflora* Sieb. (9)	S			(+)	+			+	
396	*de beuzevillei* Maiden (2)	S				(+)				
398	*stellulata* Sieber (4)	S			(+)	(+)				
	XXXII. *Piperitales* (*peppermints*)									
406	*lindleyana* DC. (1)	S			(+)	+				
407	*robertsoni* Blakely (4)	P				+				
411	*radiata* Sieb. (3)	P				+				
412	*australiana* Baker & Smith (6)	P				+				
417	*dives* Schauer (6)	P				+				
422	*andrewsi* Maiden (1)	P				+			(+)	
426	*urceolaris* Maiden & Blakely (2)	P							+	
427	*piperita* Smith (3)	P				+			+	
	XXXIII. *Psathyroxyla* (*snappy gums*)									
431	*haemastoma* Smith (2)	D			(+)	(+)			+	
434	*micrantha* DC. (2)	D			(+)	+			+	
435	*rossii* Baker & Smith (4)	D			(+)	(+)			+	

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Appendix 1 (*Continued*)

Number in Blakely (1934)	Species	Rhytidome Type*	Expanded Parenchyma in Rhytidome	Wide Phellem	Fibres with Enlarged Cross Section	Conspicuous Parenchyma Wedges	Oil Glands in Wedges	Expanded Parenchyma in Phloem	Radially Elongated Phelloderm	Kino Pockets
	XXXV. *Fruticosae*									
446	*uncinata* Turcz. (1)	D	No distinctive features observed							
	XXXVI. *Sub-buxeales*									
449	*lansdowneana* F. Muell. & J. E. Brown (1)	S	No distinctive features observed							
451	*calcicultrix* F. Muell. (1)	P	No distinctive features observed							
463	*blackburniana* Maiden (1)	P				+				
	XXXVII. *Buxeales*									
472	*bicolor* A. Cunn. (2)	P				+				+°
479	*bosistoana* F. Muell. (4)	S				(+)				
480	*behriana* F. Muell. (3)	D	No distinctive features observed							
483	*microcarpa* Maiden (1)	P				+				
484	*hemiphloia* F. Muell. (7)	P				+				+
486	*albens* Miq. (3)	P				+				+
488	*boormani* Deane & Maiden (1)	P				+			(+)	+
489	*leptophleba* F. Muell. (2)	P				(+)°				+°
492	*hillii* Maiden (2)	P	No distinctive features observed							
494	*spenceriana* Maiden (2)	P								+
505	*normantonensis* Maiden & Cambage (1)	P								+
507	*microtheca* F. Muell. (5)	P		(+)		(+)				
	XXXVIII. *Siderophloiae*									
514	*crebra* F. Muell. (2)	P		+						+
519	*jenseni* Maiden (1)	P	No distinctive features observed							
523	*siderophloia* Benth. (2)	P		+						+
525	*pruinosa* Schauer (1)	P		+						+
526	*melanophloia* F. Muell. (2)	P		+						+
533	*drepanophylla* F. Muell. (3)	P		+						+
537	*paniculata* Smith (3)	P		+						+
541	*sideroxylon* A. Cunn. (3)	P		+						+
542	*leucoxylon* F. Muell. (7)	P				+				
545	*jugalis* Naudin (1)	P		(+)		(+)				
	XXXIX. *Melliodorae*									
550	*melliodora* A. Cunn. (5)	P		+		+			(+)°	

*P = persistent rhytidome; D = deciduous rhytidome; S = semi-deciduous rhytidome.
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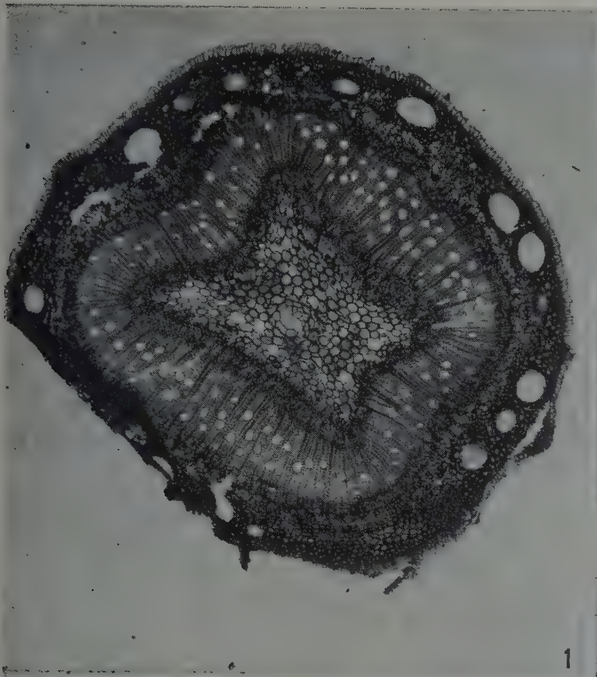
THE ANATOMY OF BARK. I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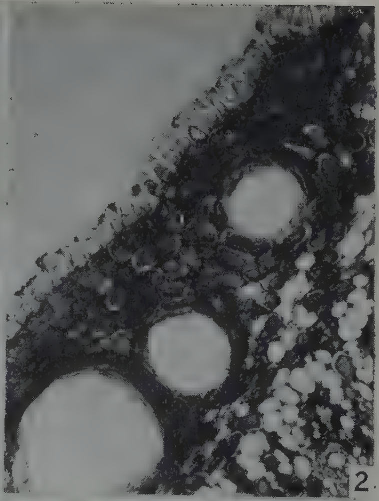
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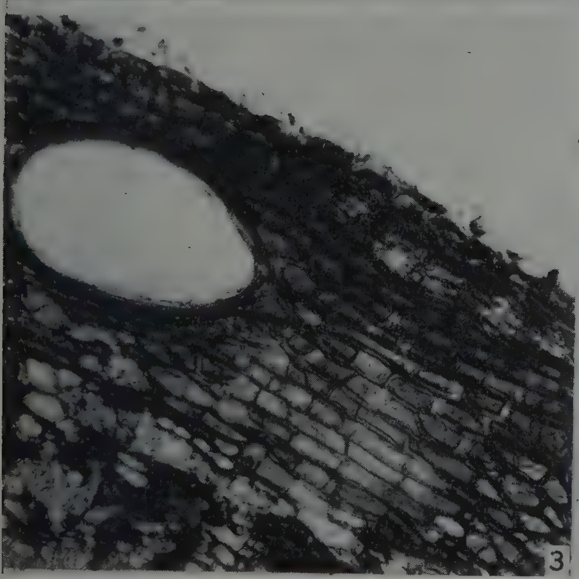
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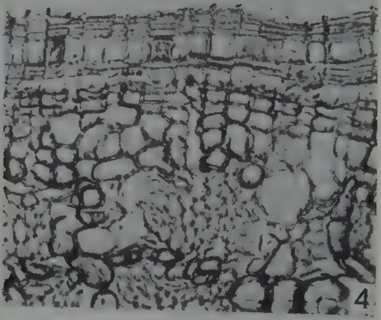
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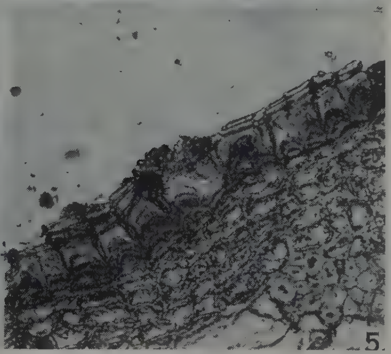
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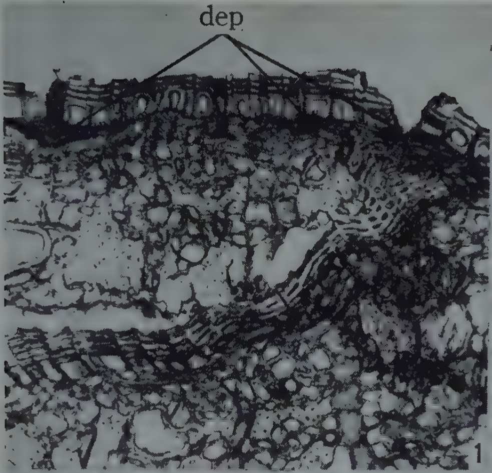

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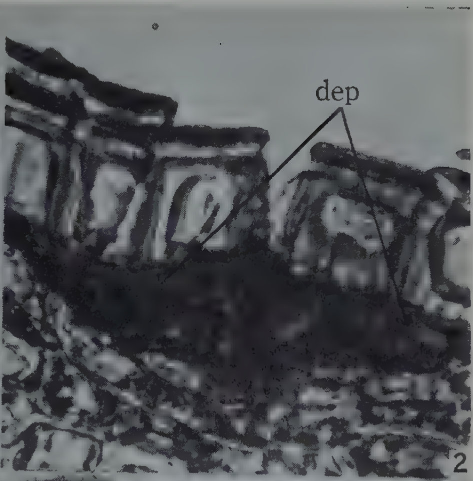

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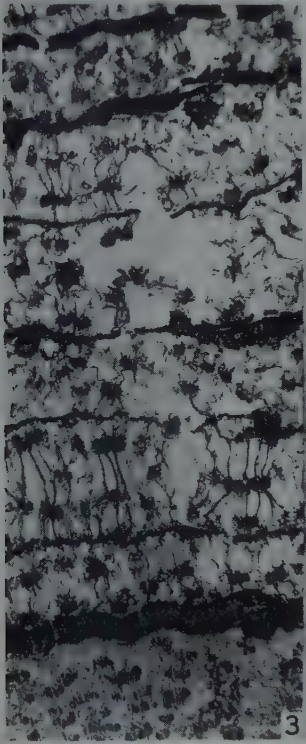

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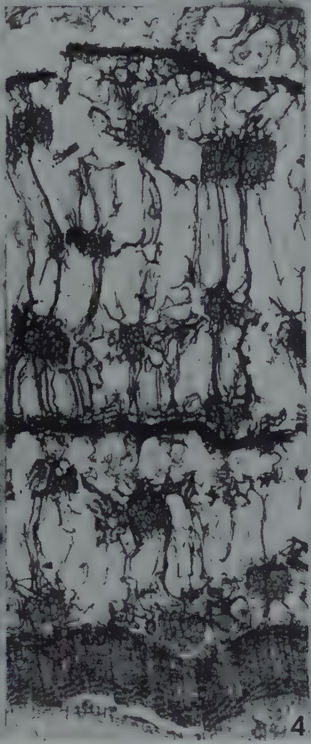

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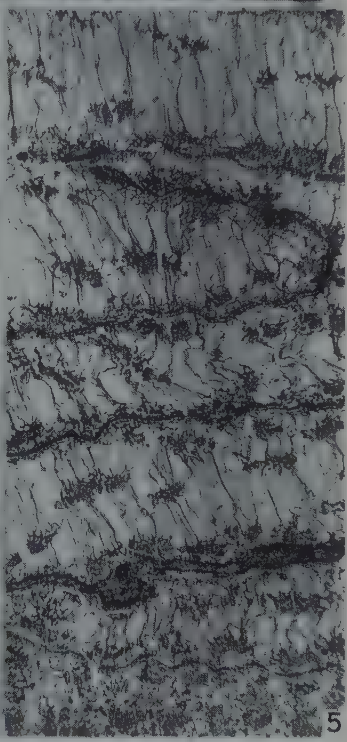

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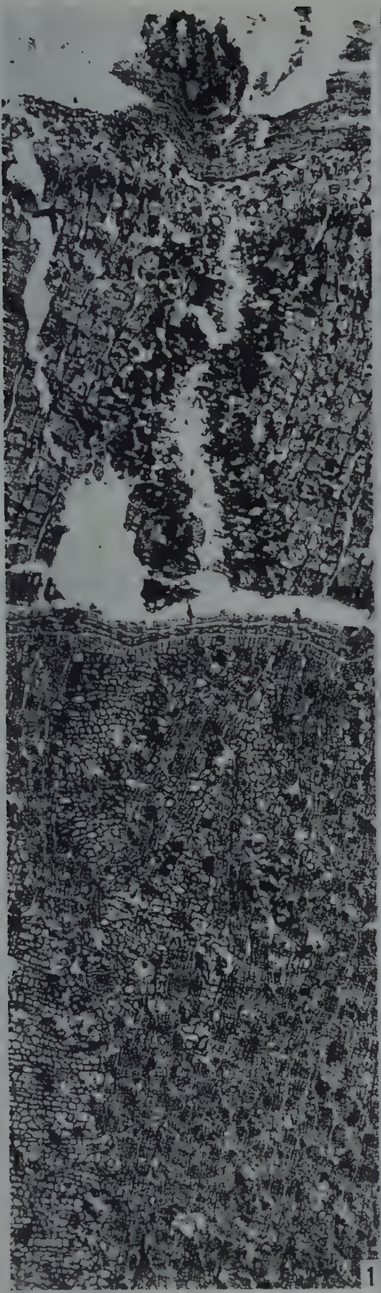

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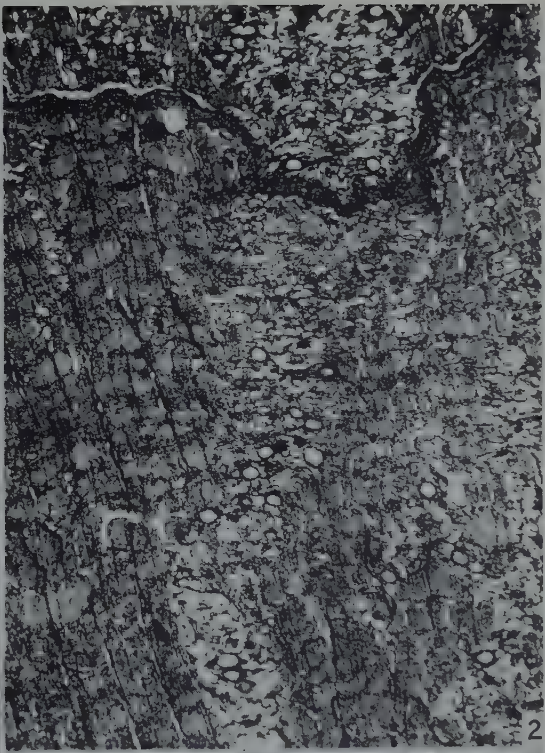

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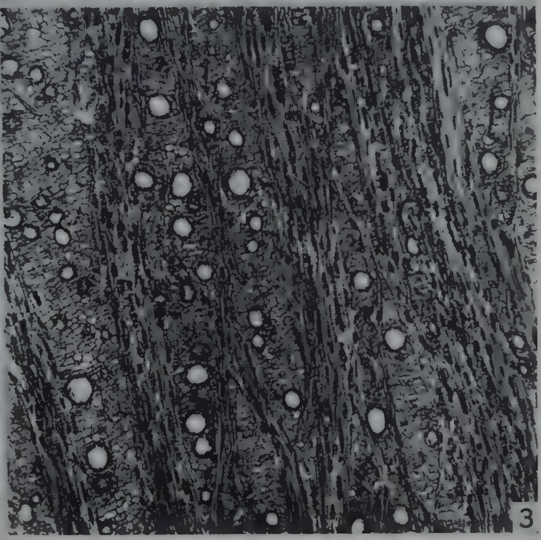

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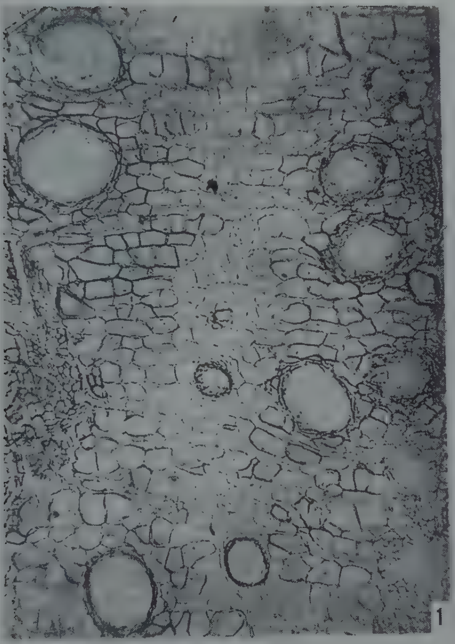
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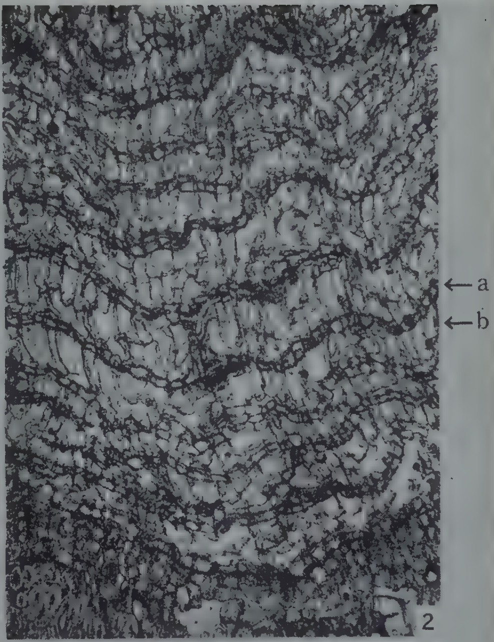

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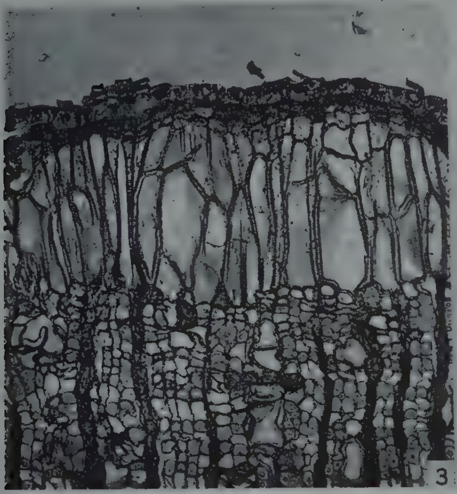
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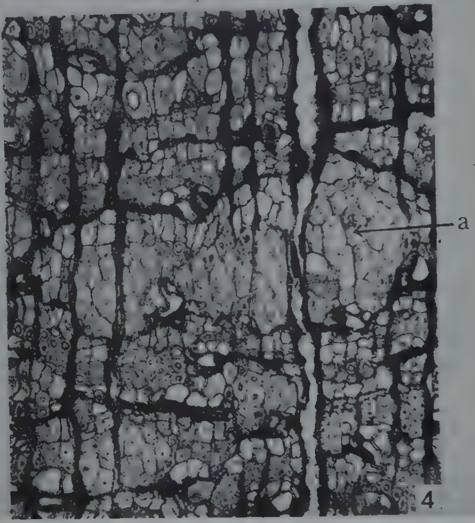

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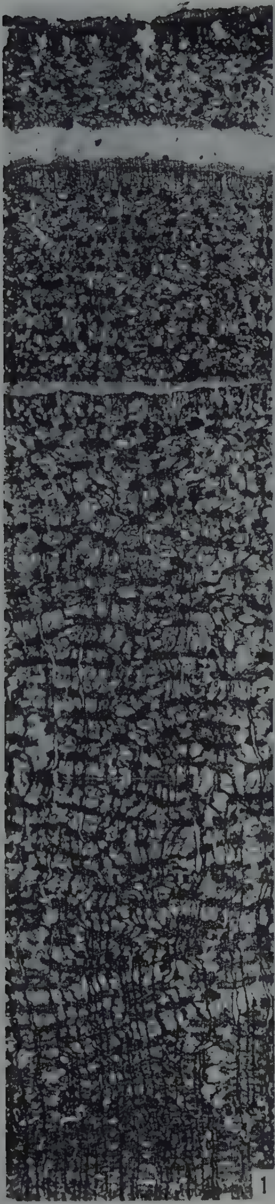
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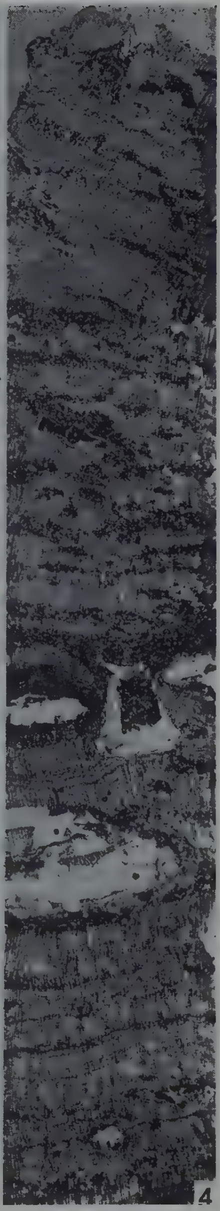
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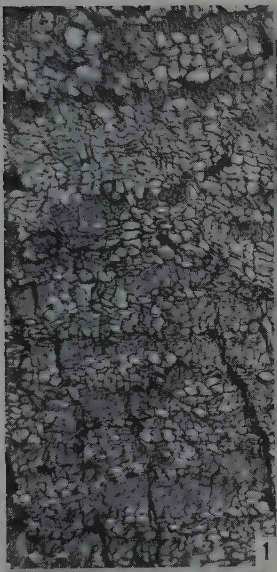
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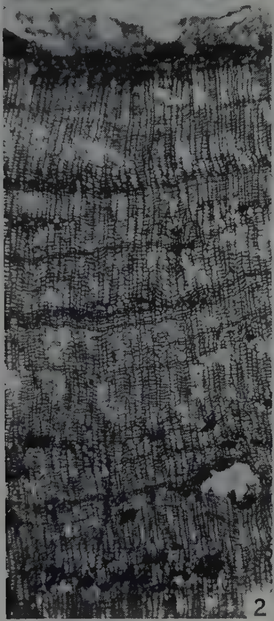
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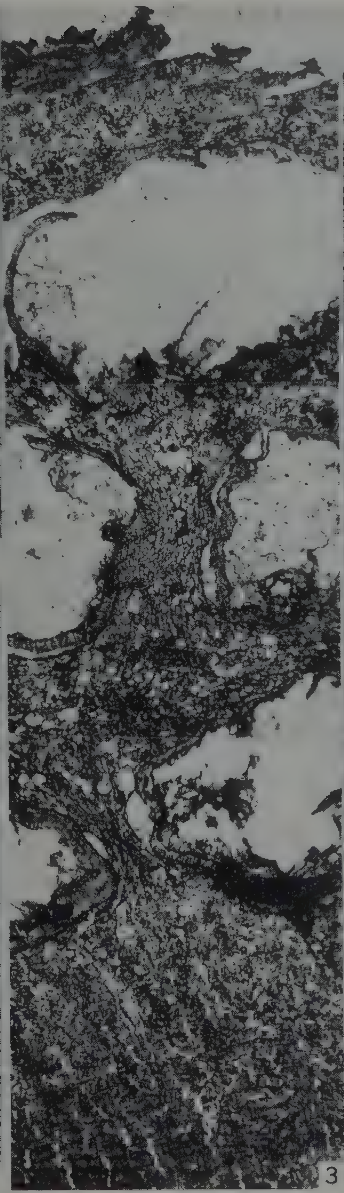
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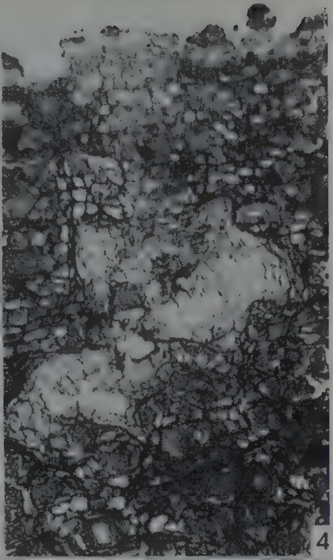
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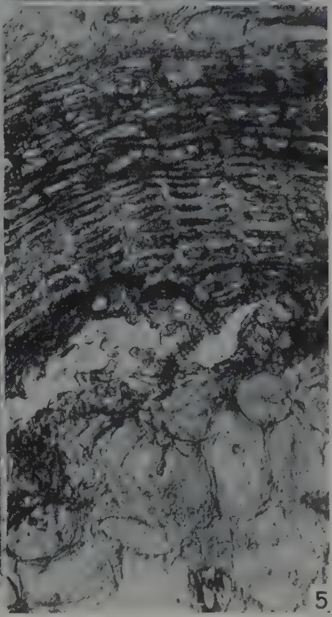
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APPENDIX 1 (*Continued*)

Number in Blakely (1934)	Species	Rhytidome Type*	Expanded Parenchyma in Rhytidome	Wide Phellem	Fibres with Enlarged Cross Section	Conspicuous Parenchyma Wedges	Oil Glands in Wedges	Expanded Parenchyma in Phloem	Radially Elongated Phelloderm	Kino Pockets
	XL. *Heterophloiae*									
555	*conica* Deane & Maiden	P	No distinctive features observed							
558	*polyanthemos* Schauer (6)	P		(+)		+			+°	
559	*baueriana* F. Muell. (3)	P				+			+°	
	XLI. *Aridae*									
561	*calycogona* Turcz. (1)	D				(+)				
564	*gracilis* F. Muell. (1)	P				(+)	+			
	XLII. *Subulatae*									
581	*transcontinentalis* Maiden (2)	D				(+)				
584	*flocktoniae* Maiden (1)	D	No distinctive features observed							
	XLIV. *Leptopodae*									
593	*salmonophloia* F. Muell. (1)	D	No distinctive features observed							

*P = persistent rhytidome; D = deciduous rhytidome; S = semi-deciduous rhytidome.

+° Indicates conflicting evidence for the feature.

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OBJECTIVE METHODS FOR THE CLASSIFICATION OF VEGETATION

II. FIDELITY AND INDICATOR VALUE

By D. W. Goodall*

[*Manuscript received December* 22, 1952]

Summary

A new index of fidelity is described, based on the ratio of frequencies for the species in two communities. The importance of significance tests in determining characteristic species is emphasized.

The value of a species as indicator of a particular community is taken as the ratio of the frequency in that community to the frequency elsewhere within the area studied. An index to express this is proposed.

The value of discriminant functions in enabling vegetation samples of uncertain affinities to be allotted to one of several possible communities is demonstrated. An example is given in which this technique has been used to determine whether one community can be regarded as intermediate between two others, or has special features of its own.

The paper is illustrated by data taken from publications of the Zürich-Montpellier school, and by original data collected in the Victorian Mallee.

I. INTRODUCTION

The concept of fidelity has attracted less attention than it deserves from plant ecologists outside the Swiss school in which it originated. It is closely bound up with the concept of characteristic species. This idea was introduced by Gradmann in 1909 and was developed by Braun-Blanquet to provide the foundation stone for his general system of plant sociology. Plant communities were classified according to the presence or absence in them of small groups of "characteristic" species much more common in one particular community than in any other. The degree to which a species was characteristic was recognized by Braun-Blanquet as a property showing continuous variation and to this property he gave the name fidelity. No attempt was made to express it quantitatively; the fidelity of a species in (or to) a particular community was simply expressed in one of five grades, loosely defined as follows:

(1) Strange (*fremde*); species that are rare and accidental intruders from another plant community or relics of a preceding community.

(2) Indifferent (*vage*); species without pronounced affinities for any community.

(3) Preferential (*holde*); species present in several communities more or less abundantly but predominantly or with better vitality in one certain community.

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* Botany Department, University of Melbourne. Present address: University College of the Gold Coast, Achimota, Gold Coast.

(4) Selective (*feste*); species found most frequently in a certain community but also, though rarely, in other communities.

(5) Exclusive (*treue*); species completely, or almost completely, confined to one community.

Clearly such verbal definitions give considerable scope for disagreement in allotting a grade to a particular species in a particular community, even where the same stands of the various communities are under consideration. A somewhat more precise meaning was given to these five grades of fidelity by Szafer and Pawlowski (1927) in a chart reproduced by Braun-Blanquet (1928). This chart depends on data for "presence" and for abundance on the five-point scale used by Braun-Blanquet and his school, in the association in question and in all other associations. For instance, the exclusive species are defined in this chart as those present in more than 60 per cent. of the stands of the association in question and covering at least one-quarter of the area, but in other associations not present in more than 40 per cent. of the stands nor covering 5 per cent. of the area; or, if covering no more than one-quarter of the area in the association in question although present in 60 per cent. or more of the stands, then in other associations not present in more than 20 per cent. of the stands or covering more than 25 per cent. of the area; or, finally, if not present in more than 60 per cent. of the stands of the association in question, then in order to be ascribed to this grade of fidelity the species must be lacking or very rare in all other associations.

Though Braun-Blanquet has always regarded characteristic species as of the highest importance in the classification of vegetation, these grades of fidelity have never occupied a prominent place in description of particular communities. In recent publications from his school, no attempt is made to distinguish different grades of fidelity among the characteristic species.

Braun-Blanquet developed the concept of fidelity in relation to associations; but he subsequently extended it to alliances and orders, the higher units of his vegetational hierarchy, defined like the association on a group of characteristic species.

Fidelity is generally a more useful concept when applied within a specified universe of discourse than as an absolute term. Though doubtless some species are confined under all circumstances to a particular community, one generally needs to talk rather of those which within a particular region or in particular types of vegetation are confined to that community. For the former, Braun-Blanquet uses the expression "regional fidelity"; for the latter he has no special phrase, though it is clearly involved, for instance, in his recognition of differential species.

The method proposed by Braun-Blanquet for determining degrees of fidelity depends, as has been said, on both "presence" and abundance. Abundance in turn, in Braun-Blanquet's "total estimate," depends only on cover where this exceeds 25 per cent., but below this depends also on density. The degree of fidelity is thus highly composite, depending on three variables largely independent of one another, and with density based on inadequate verbal descriptions ("spärlich," "zahlreich," etc.) rather than definitions. Such an index clearly does not lend itself to exact treatment. Indeed, any such composite index is bound to be largely arbitrary; the relative importance ascribed to the different variables involved determines the weight given to them, and for this there is no objective criterion. A species may show its "preference" for one community rather than others by greater constancy, greater density, or a higher percentage cover; while the three usually go together, there is no necessary connexion between them, and conclusions based on one type of measurement may sometimes be at variance with those based on another.

In deriving an index of fidelity which will reflect the continuous variation in the feature it measures, and which will be capable of reasonably exact treatment, it therefore seems preferable to base it upon one type of measurement only. Those which immediately suggest themselves are constancy and frequency.* These are not, in general, measures of the quantity of the species present. But where fidelity is to be compared between species they are probably to be preferred to quantitative measures; a small ephemeral which occurs in one community to the extent of one or two individuals in each quadrat studied, and is found nowhere else, may reasonably be regarded as more characteristic of that community than a tree which likewise occurs in every quadrat of the same community and less frequently elsewhere, even though the cover and dry weight of the tree exceed those of the ephemeral by a factor of many thousand. Furthermore, if one uses such measures as dry weight, cover, or density it is necessary either to deal with data seriously skewed by a large number of zero records, or to restrict attention to that part of the data where the species in question occurs.

II. An Index of Fidelity

The problem of selecting an index of fidelity if only frequency data are to be considered may be regarded as analogous with that of choosing an index of association between two species—a question discussed by Dice (1945), Cole (1949), and Nash (1950). The figure obtained should express the extent to which the frequency in the community in question exceeds that in whichever other community approaches it most nearly. The data can be set out as a 2×2 table (Table 1), where a, b, c, and d represent the numbers of stands or quadrats in each category. The significance of the difference in the ratios

$$\left(\frac{a}{a+c} - \frac{b}{b+d}\right),$$

that is, of the difference in frequencies, may be readily determined by the χ^2 test, or, where one or more of the numbers is small, by the exact calculation of P using the method given by Fisher (1937). Since, however, community A has

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* "Presence," constancy, and frequency are alike in that all are measures of probability; "*presence*" is the probability of encountering the species within any single stand, and *constancy* that of finding it a quadrat of specified size within any stand chosen at random, while *frequency* is the probability of finding it in a quadrat of specified size within a particular stand. If the differences between different stands are no greater than between different parts of the same stand, constancy and frequency are equivalent; "presence" is not strictly comparable, since it involves the distribution of stand size.

ex hypothesi a higher frequency than community B, only half the distribution is being considered and the value for P should be doubled.

Though the significance of the difference may easily be calculated in this way, it does not lead directly to a convenient index of fidelity. The value of χ^2 or of P found will depend on the number of observations in each community as well as on the relationship between the frequencies. One may eliminate this dependence and obtain a convenient index of the association of the species with community A, within this pair of communities, by computing

$$\sqrt{\frac{\chi^2}{N}},$$

which is distributed very nearly as the correlation coefficient r for N degrees of freedom where N is large. It therefore lends itself very well to direct determination of significance.

TABLE 1

	Community		Total
	A	B	
Species x present	a	b	$a+b$
Species x absent	c	d	$c+d$
Total	$a+c$	$b+d$	$a+b+c+d=N$

But, as Cole (1949) has pointed out, this index of association can reach its maximum of unity only if $b=c=0$—if, that is, the total number of records for the species and for the community are the same. Clearly, this is unsatisfactory in an index of fidelity; a rare species can reach as high a degree of fidelity (in Braun-Blanquet's sense, and as the term is naturally understood) as a common one, and the number of records of the community should not affect the index.

To avoid the corresponding difficulty in interspecific association, Cole has suggested an index which may be expressed in the form

$$\frac{a-a^1}{A-a^1},$$

where a^1 is the expectation for the first cell of Table 1, viz.:

$$\frac{(a+b)(a+c)}{(a+b+c+d)},$$

and A the maximum possible value of it —$(a+b)$ or $(a+c)$, whichever is smaller. This would not be so appropriate as an index of fidelity, however, since it would express association of the community with the species as well as association of the species with the community, only the latter being implied in the concept of fidelity.

Accordingly it is suggested that the *difference in frequency* (or constancy or "presence") in the two communities expressed *as a proportion of the lesser value* (i.e. of the value for community B), after Yates's correction for continuity* has been applied, be used as an index of fidelity, viz.:

$$\frac{(a-\frac{1}{2})(b+d)}{(b+\frac{1}{2})(a+c)}-1\,.$$

This index, values of which are set out in Table 2 for comparison with Cole's index, will take a value of zero where the species has equal frequencies in the two communities, ranging up to indefinitely high values where it is strictly confined to one community. The inclusion of Yates's correction is desirable, since otherwise one is confronted, for instance, with the anomaly of a species having infinite fidelity where only a single record of it exists. If values less than zero occur, they may be quoted as zero; they are due to the correction erring on the conservative side. The correction is also responsible for the failure of the values in Table 2 to reflect the exact ratio of 2 : 1 in the observed frequencies; if these hypothetical data were samples of populations in which, taken as a whole, this ratio held, then as the sample sizes increased the values of the index would in each case approach unity as a limit.

TABLE 2

EFFECT OF RELATIVE COMMONNESS OF COMMUNITIES ON INDICES OF FIDELITY

Case	I			II			III		
Community	*A*	*B*	Total	*A*	*B*	Total	*A*	*B*	Total
Quadrats with species *x*	600	300	900	60	300	360	600	30	630
Quadrats without species *x*	400	700	1100	40	700	740	400	70	470
Total	1000	1000	2000	100	1000	1100	1000	100	1100
Cole's index	0·333			0·405			0·476		
Proposed index	0·995			0·980			0·966		

The sampling error of the proposed index has not been studied, and it is not suggested that it should be used in significance tests; it is intended purely for expressing fidelity in quantitative terms. This purpose it will serve very well; if, for instance, the fidelity index is 0.5, then the chance of encountering the species in the community in question is half as great again as in any other community. Significance should, of course, always be tested—but this should be done independently, using either χ^2 or the exact method.

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* This correction consists in adding half a unit to values below expectation and subtracting it from those above. The need for it results from the fact that a continuous variable (the probability of encountering the species) is represented in a sample only by an integral value (the number of times it is in fact encountered).

The use of this index may first be illustrated on data employed by Braun-Blanquet himself (1925) to show the use of the terms "feste" and "holde" as grades of fidelity. Two species occurred only in two associations; the first, species *A*, occurred in 11 out of 15 stands of association I, in five out of 15 in association II. Applying the formula above, we find a fidelity index of 0.91, with a probability of 0.07. The difference in "presence" of this "feste" species thus does not quite reach significance, and if fidelity is to be based only on "presence" species *A* cannot properly, on the basis of these data alone, be regarded as characteristic of association I. But Braun-Blanquet includes consideration of quantity in assessing fidelity; if then we look at the data for abundance, we find that all the records in association II are cited as "+", whereas seven out of the 11 records in association I exceed this level. The probability of this difference arising by chance is 0.09, so taking this together with the differences in "presence" one may accept species *A* as being significantly more characteristic of association I than II. Species *B*, on the other hand, is always recorded as "+"—in eight stands of association I and four of II; the fidelity index is 0.67, but the probability of this difference arising by chance is 0.24—considerably too high to justify regarding species *B* as even a "holde" characteristic species of association I.

In Table 3, the use of the fidelity index is illustrated on further more recent data from Braun-Blanquet's school. Tchou Yen-Tcheng (1948-9) published an extensive account of forests in the river valleys of Languedoc. For the Populetum albae with which he was mainly concerned, he included an association table of 40 stands; for the seven other associations described, data for from nine to 26 stands were included—in some cases apparently incomplete, being without records of any "accidental" species. Eighteen species are regarded as regionally characteristic of the Populetum albae; in Table 3 they are listed, with their "presence" in this association, their highest "presence" in any other association, the fidelity index computed as described above, and the value of *P* computed by the exact test. For the four species which occur in no other association, the question of which association to use for comparison presents some difficulty. If relationships between associations and species were ignored, the highest probability that the species was present in the association but missing from the recorded stands would be in the association of which there were fewest records—the Glaucieto-Scrophularietum caninae. But it seems more reasonable to take the observed relationships into account, and use for comparison the association which has most affinity with the Populetum albae. On the data presented, this is the Alneto-Fraxinetum oxycarpae—with the highest "presence" outside the Populetum albae for seven species "characteristic" of this association.

The low levels of significance in Table 3 are noteworthy; only for one species, *Carex pendula*, is the "presence" clearly different in the two associations, though for *Iris foetidissima* and *Acer negundo* the difference just reaches the 5 per cent. significance level. The most surprising thing, however, is that five of the 18 species have higher "presence" in some other association than in the Populetum albae. Study of the abundance-dominance index in the tables does not always shed light on these discrepancies. *Torilis arvensis*, for instance, is allotted grade 1 in 10 per cent. of the records for Populetum albae, and in 13 per cent. of the records for Saponarieto-Salicetum purpureae, and grade "+" in 30 and 37 per cent. respectively; yet it is included as a characteristic species of the former. *Cucubalus baccifer* in Populetum albae attains grade 2 in 8 per cent., grade 1 in 18 per cent., and "+" in 20 per cent. of the records; in the Saponarieto-Salicetum purpureae the corresponding figures are 6, 31, and 6 per cent. Again it is not clear from the published data why the species is regarded as characteristic of the Populetum albae.

TABLE 3

FIDELITY OF THE CHARACTERISTIC SPECIES OF THE POPULETUM ALBAE IN BAS-LANGUEDOC

Date of Tchou Yen-Tcheng (1948-9)

Species	"Presence" in Populetum albae		Greatest "Presence" Elsewhere			Fidelity Index	P†
	No.	Per cent.	Association*	No.	Per cent.		
Fraxinus oxycarpa Willd.	40	100	*A*	9	90	0·04	0·40
Ulmus campestris L.	36	90	*A*	6	60	0·36	0·08
Populus alba L.	30	75	*A*	5	50	1·34	0·25
Bryonia dioica Jacq.	19	48	*A*	6	60	0·00	1·00
Iris foetidissima L.	17	43	*S*	2	13	1·64	0·05
Carex pendula Huds.	16	40	*S*	1	6	3·14	<0·01
Cucubalus baccifer L.	18	45	*S*	7	44	0·00	1·00
Euphorbia amygdaloides L. var.	17	43	*S*	7	44	0·00	1·00
Torilis arvensis (Huds.) Link	16	40	*S*	8	50	0·00	1·00
Acer negundo L.	14	35	*S*	1	6	2·60	0·05
Pastinaca opaca Bernh. ex Hornem.	14	35	*A*	4	40	0·00	1·00
Ficaria calthaefolia Reichb.	9	23	*H*	4	19	0·00	0·83
Viola odorata L. ssp. *jucunda*	8	20	*A*	2	20	0·00	1·00
Lithospermum officinale L.	5	13	*A*	0	0	1·25	0·62
Vinca major L.	4	10	*A*	0	0	0·75	0·79
Sison amomum L.	3	8	*A*	0	0	0·25	1·00
Symphytum tuberosum L.	3	8	*A*	2	20	0·00	1·00
Viburnum opulus L.	2	5	*A*	0	0	0·00	0·73

*Other associations *A*: Alneto-Fraxinetum oxycarpae (10 records)
H: Holoschoenetum (21 records)
S: Saponarieto-Salicetum purpureae (16 records).

†*P* gives the probability that the observed "presence" in one or other of the associations compared would equal or exceed that observed for Populetum albae, on the assumption that the true "presence" values are equal.

A second example may be taken from the data of Adriani (1945) for the Artemisietum maritimae in Holland (22 stands). The characteristic species of this give the figures shown in Table 4.

Here the grounds for regarding *Obione portulacoides* and *Artemisia maritima* as characteristic are evident, but the case for *Statice limonium* is less clear. Even if the data which Adriani tabulates separately for the *Statice limonium* facies of the association are included, the difference for this species does not become significant ($P = 0.06$), and the difference for *Obione portulacoides* then ceases to be significant ($P = 0.06$).

TABLE 4

FIDELITY OF THE CHARACTERISTIC SPECIES OF THE ARTEMISIETUM MARITIMAE IN HOLLAND

Data of Adriani (1945)

Species	"Presence" in Artemisietum maritimae		Greatest "Presence" Elsewhere			Fidelity Index	P
	No.	Per cent.	Association*	No.	Per cent.		
Obione portulacoides (L.) Moq.	20	91	*P*	13	54	0·57	0·01
Statice limonium L.	19	86	*P*	16	67	0·22	0·17
Artemisia maritima L.	18	82	*A*	4	16	3·42	<0·01

*Other associations *P*: Puccinellietum maritimae (24 records)
A: Armerieto-Festucetum arenariae (25 records).

The explanation of these discrepancies is doubtless the fact that the association tables published by the Zürich-Montpellier school represent only a part of the observations made; the conclusions reached may be based on much wider acquaintance with the vegetation, and the tables are probably intended to illustrate these conclusions rather than to justify them. If this were not so, it would clearly be meaningless to include as characteristic a species recorded once only—as is done by Tchou Yen-Tcheng with *Lathraea clandestina* L. in the Saponarieto-Salicetum purpureae and by Adriani with *Obione pedunculata* (L.) Moq. in the Puccinellietum maritimae. The latter case seems to derive from the original description of the association by Braun-Blanquet and Leeuw (1936), *Obione pedunculata* being included in three of the four stands they recorded for this association. But even if the records of Braun-Blanquet and Leeuw are combined with those of Adriani for the Puccinellietum maritimae and the Artemisietum maritimae, the difference in the "presence" of *O. pedunculata* in the two associations remains non-significant ($P = 0.15$).

As a third example of the use of the index of fidelity, one may take the vegetation of a small area of the Victorian Mallee. Data were collected on the species present in 256 25-sq. m quadrats distributed over an area 640 m square, and the interspecific correlations were used to classify these quadrats into four communities (Goodall 1953, Table 1). Table 5 gives the index of fidelity and associated P value for each species, in that community where it attained its highest frequency. The indices of fidelity are restricted in their application, of course, to the area from which the data were collected and it would not be claimed that they necessarily have any wider relevance.

TABLE 5

FIDELITY OF "CHARACTERISTIC" SPECIES IN FOUR COMMUNITIES IN A SMALL AREA OF THE VICTORIAN MALLEE

Quadrats 5 m square

Species	No. of Records	Index of Fidelity	*P*
Cassia eremophila grouping (17 records)			
Acacia microcarpa F. Muell.	1	0·01	0·69
Atriplex stipitata Benth.	3	7·63	0·02
†*Bassia uniflora* (R. Br.) F. Muell.	17	0·00	1·00
Beyeria opaca F. Muell.	1	0·00	0·84
†*Cassia eremophila* A. Cunn.	17	33·94	<0·01
Cassia sturtii R. Br.	2	14·88	0·04
Enchylaena tomentosa R. Br.	4	3·88	0·08
Eremophila glabra (R. Br.) Ostenf.	1	4·29	0·32
†*Eucalyptus oleosa* F. Muell.	17	0·19	0·06
Grevillea huegelii Meiss.	6	2·88	<0·01
Kochia pentatropis R. Tate	4	3·04	0·02
Olearia muelleri Benth.	10	8·14	<0·01
Santalum murrayanum F. Muell.	2	0·66	0·42
Stipa elegantissima Lab.	2	1·26	0·30
S. multispiculis J. M. Black	1	0·63	0·57
S. variabilis Hughes	15	0·00	0·62
Trichinium seminudum J. M. Black	2	8·14	0·24
Westringia rigida R. Br.	12	9·21	0·01
Zygophyllum apiculatum F. Muell.	11	0·31	0·17
Bassia uniflora grouping (90 records)			
Acacia pycnantha Benth.	1	0·00	1·00
Bassia parviflora Anders.	4	0·29	0·51
†*B. uniflora* (R. Br.) F. Muell.	90	0·00	1·00
Cassytha melantha R. Br.	1	0·00	1·00
Chenopodium desertorum J. M. Black	1	0·00	1·00
**C. pseudomicrophyllum* Aellen	32	1·00	<0·01
Dodonaea stenozyga F. Muell.	5	1·77	0·23
Eucalyptus calycogona Turcz.	27	0·43	0·29
Kochia tomentosa (Moq.) F. Muell.	4	5·46	0·14
Lolium perenne L.	1	0·00	1·00
Olearia pimelioides Benth.	1	0·00	1·00
Pittosporum phillyraeoides D.C.	4	5·46	0·14
Stipa mollis R. Br.	9	0·21	0·35
Trichinium exaltatum Benth.	1	0·00	1·00
Dodonaea bursariifolia grouping (66 records)			
Acacia rigens A. Cunn.	3	0·26	0·54
A. sclerophylla Lindl.	2	0·00	0·70
Callitris verrucosa R. Br.	17	12·83	<0·01
Cryptandra tomentosa Lindl.	1	0·00	0·99
Dianella revoluta R. Br.	2	0·26	0·66
Dodonaea bursariifolia Behr.	47	0·31	0·06
†*Eucalyptus dumosa* A. Cunn.	66	0·26	<0·01
Gahnia lanigera (R. Br.) Benth.	1	0·26	0·89

TABLE 5 (*Continued*)

Species	No. of Records	Index of Fidelity	*P*
Dodonaea bursariifolia grouping (66 records)—cont.			
Halgania cyanea Lindl.	2	0·26	0·66
Helichrysum catadromum N. A. Wakefield	2	2·77	0·39
Hibbertia stricta R. Br.	2	0·26	0·66
H. virgata R. Br.	1	0·26	0·89
Lepidosperma viscidum R. Br.	6	3·61	0·05
Lomandra leucocephala (R. Br.) Ewart	5	0·62	0·33
Melaleuca pubescens Schau.	5	0·62	0·33
Micromyrtus ciliatus J. M. Black	6	12·83	0·01
Myoporum platycarpum R. Br.	3	0·26	0·54
Phebalium glandulosum Hk.	1	0·00	0·99
Prostanthera microphylla A. Cunn.	1	0·26	0·89
Schoenus aphylla Boeck.	1	0·26	0·89
†*Triodia irritans* R. Br.	66	0·26	<0·01
Vittadinia triloba grouping (83 records)			
Baeckia behrii F. Muell.	3	0·33	0·62
Danthonia semiannularis R. Br.	17	1·75	0·01
Melaleuca uncinata R. Br.	46	0·39	0·05
Vittadinia triloba D.C.	38	0·21	0·22
Vulpia myuros (L.) Gmel.	4	4·44	0·19

*Both forms of *C. pseudomicrophyllum* (see Goodall 1953) have been considered together.

†These species were involved in the definition of the grouping in question.

On the basis of the data in Table 5, one may tentatively name the following species as characteristic of the four communities:

Cassia eremophila grouping: *Atriplex stipitata*
Cassia eremophila
Cassia sturtii
Grevillea huegelii
Kochia pentatropis
Olearia muelleri
Westringia rigida

Bassia uniflora grouping: *Chenopodium pseudomicrophyllum*

Dodonaea bursariifolia grouping: *Callitris verrucosa*
Eucalyptus dumosa
Lepidosperma viscidum
Micromyrtus ciliatus
Triodia irritans

Vittadinia triloba grouping: *Danthonia semiannularis*
Melaleuca uncinata

The index of fidelity proposed here has been devised for use with frequency (constancy, "presence") data. But it could easily be modified for use with other types of data. The ratio of any quantitative measure of a species in the community where it is greatest to that next on the list could be used as an index of fidelity. Here, however, difficulties may arise in testing significance. If the quantitative measure used, or some transform of it, is normally distributed the t test may be applied; otherwise a rigorous test may not be possible. A fidelity index based on a quantitative measure would, it is true, have the advantage over one based on frequency and similar measures that it would be independent of quadrat size. The dependence on quadrat size of the index used above makes it desirable always to state the quadrat size in connexion with it.

III. Indicator Value

It may sometimes be useful to consider the constancy or frequency of a species in a particular community, not as distinguishing it simply from whichever other community contains that species most frequently, but as distinguishing it from all other communities occurring in the area, considered collectively. Though a species has very low fidelity, on account of the presence in the area of two associations in which it occurs equally, it may nevertheless be a very good index of this pair of associations as against all others. This situation is covered by Braun-Blanquet's recognition of fidelity to alliances and orders if the two associations in question are included in the same higher unit. If they are not, then the value of the species in indicating the community is not recognized as fidelity.

The term *indicator value* may be used to express the frequency (constancy, "presence") of a species in a particular community, compared with all other communities considered. As an index of indicator value, one exactly parallel with that of fidelity may be used. A negative indicator (one consistently *less* frequent in one community than in others) may be as valuable as a positive indicator, so negative values of this index have a meaning which they lacked in relation to fidelity.* Accordingly, it is suggested that the same formula for the index of indicator value be used as for the index of fidelity, a being taken as the number of records in which the species appears either in the particular community in question, or in all other communities considered, whichever has the higher frequency; in the former case a positive sign is attached to the index, in the latter a negative sign. For instance, in the data for the Victorian Mallee discussed above, *Eucalyptus dumosa* is absent from all but two of the 17 quadrats of the *Cassia eremophila* grouping, but present in 168 of the 239 quadrats in other groupings. The table thus reads:

$$a = 168,\ b = 2$$
$$c = 71,\ d = 15$$

and the index of indicator value is:

$$\frac{(168-\frac{1}{2})(2+15)}{(2+\frac{1}{2})(168+71)} - 1 = 3.77.$$

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* It is conceivable that a widespread species might be missing from, or uncommon in, one community only within an area studied; in this case it could be said to have negative fidelity to that community. But it would be rare for such "negative fidelity" to reach significance; even the commonest species is generally absent from more than one community.

Since *Eucalyptus dumosa* is *less* frequent in the *Cassia eremophila* grouping than in others, this is read as

$$-3.77.$$

Once again, the significance of each value needs to be determined independently, by χ^2 or the exact test.

In Table 6, indices of indicator value, and their significance, have been computed for the quadrat data from the Victorian Mallee already discussed, in all species for which one of the four indices reaches significance. It is somewhat surprising that this is true of so many species; of the 47 species occurring in more than one quadrat, more than half—28—have appreciable indicator value on this test. Most of the other species are infrequent—only one (*Stipa mollis*) was recorded in more than eight quadrats. It is not surprising that the six species on which the groupings were based have a significant indicator value for all groupings; but is noteworthy that this is also true for three other species —*Dodonaea bursariifolia, Melaleuca uncinata,* and *Zygophyllum apiculatum.* These results support the view that the four groupings are in fact natural assemblages of species—at least within the limited area studied.

A table of indicator values such as Table 6 may be used as an approximate method for allocating a quadrat of uncertain affinities to the most appropriate community (a more exact method using the presence or absence of a few species only is discussed in the next section, but it would be too laborious where many species were taken into account). For all the species present in the quadrat, the indicator values are summed for each community in turn, and the community for which the sum is largest is that to which the quadrat should be allotted. For instance, consider a quadrat containing *Dodonaea bursariifolia, Eucalyptus dumosa, E. oleosa, Stipa variabilis,* and *Vittadinia triloba.* The sums of the indicator values in the four communities are:

Cassia eremophila grouping: $-22.32-3.77+0.78+0.43-0.23=-25.11$

Bassia uniflora grouping: $-2.17-1.05+0.80+0.47+0.21=-1.76$

Dodonaea bursariifolia grouping: $+1.25+0.80-1.75-107.73-2.45=-109.88$

Vittadinia triloba grouping: $+0.46+0.34-0.22+0.76+0.76=+2.10.$

There is thus little doubt that a quadrat containing these species should be allotted to the last community.

IV. The Use of Discriminant Functions

A method has been devised by Fisher (1936) for finding the most appropriate way in which to combine a number of measurements to determine to which of two classes a particular individual is most appropriately allotted. The linear function of the measurements used is called a *discriminant function.* This method has been used in such fields as physical anthropology and plant taxonomy, but does not yet seem to have reached application in plant sociology. Yet it is very apposite here. Let us consider the case where two associations are well recognized, and much information about the constancy and quantity of different species present in them is available; one is now presented with data

TABLE 6

INDICATOR VALUE OF SPECIES IN RELATION TO DIFFERENT COMMUNITIES IN THE VICTORIAN MALLEE. QUADRATS 5 M SQUARE

Species	Grouping											
	Cassia eremophila			*Bassia uniflora*			*Dodonaea bursariifolia*			*Vittadinia triloba*		
	No. of Records	Index	*P*	No. of Records	Index	*P*	No. of Records	Index	*P*	No. of Records	Index	*P*
Atriplex stipitata	3	22·43	<0·01	1	0·00	1·00	0	−1·43	0·60	0	−2·36	0·41
*Bassia uniflora**	17	1·16	<0·01	90	3·79	<0·01	3	−10·96	<0·01	14	−2·62	<0·01
Callitris verrucosa	0	−1·49	0·56	0	−17·98	<0·01	17	31·67	<0·01	1	−4·28	0·01
*Cassia eremophila**	17	388·40	<0·01	2	−2·80	<0·01	0	−12·55	<0·01	1	−4·92	<0·01
C. sturtii	2	11·29	0·01	0	−0·63	0·84	0	−0·04	1·00	0	−0·44	0·91
Chenopodium pseudomicrophyllum (I)†	1	−0·17	0·92	20	4·53	<0·01	1	−4·67	<0·01	4	−1·29	0·05
C. pseudomicrophyllum (II)†	1	−0·02	1·00	12	0·84	0·10	0	−14·63	<0·01	10	0·47	0·01
Danthonia semiannularis	0	−2·93	0·28	6	−0·71	0·12	4	−0·74	0·15	17	1·99	<0·01
Dodonaea bursariifolia	0	−22·32	<0·01	15	−2·17	<0·01	47	1·25	<0·01	44	0·46	0·01
D. stenozyga	0	0·00	1·00	5	4·53	0·04	0	−2·47	0·33	1	−0·44	0·55
Enchylaena tomentosa	4	6·57	<0·01	3	−0·01	0·51	0	−5·60	0·10	3	0·00	1·00
Eucalyptus calycogona	3	0·00	1·00	27	1·17	<0·01	7	−0·92	0·35	12	−0·40	0·12
*E. dumosa**	2	−3·77	<0·01	35	−1·05	<0·01	66	0·80	<0·01	67	0·34	<0·01
*E. oleosa**	17	0·78	<0·01	73	0·80	<0·01	16	−1·75	<0·01	41	−0·22	0·04
Grevillea huegelii	6	4·73	<0·01	4	−0·75	0·17	5	0·00	1·00	4	−0·55	0·24
Kochia pentatropis	4	4·79	<0·01	6	0·56	0·27	0	−6·99	0·05	2	−0·82	0·27
K. tomentosa	0	0·00	1·00	4	11·91	0·03	0	−1·43	0·60	0	−2·36	0·41
Lepidosperma viscidum	0	0·00	1·00	0	−6·05	0·09	6	9·56	<0·01	1	−0·76	0·43
Melaleuca uncinata	0	−10·88	<0·01	3	−11·47	<0·01	35	1·01	<0·01	46	1·46	<0·01
Micromyrtus ciliatus	0	0·00	1·00	0	−5·19	0·14	6	30·67	<0·01	0	−4·28	0·19
Olearia muelleri	10	13·06	<0·01	5	−0·33	0·29	0	−2·12	<0·01	4	−0·55	0·24
Pittosporum phillyraeoides	0	0·00	1·00	4	11·91	0·03	0	−1·43	0·60	0	−2·36	0·41
*Stipa variabilis**	15	0·43	0·02	70	0·47	<0·01	0	−107·73	<0·01	72	0·76	<0·01
Trichinium seminudum	2	7·44	0·04	0	−2·80	0·35	0	−1·43	0·60	2	0·25	0·58
*Triodia irritans**	1	−5·33	<0·01	3	−19·37	<0·01	66	1·71	<0·01	65	0·91	<0·01
Vittadinia triloba	4	−0·23	0·23	33	0·21	0·11	7	−2·45	<0·01	38	0·76	<0·01
Vulpia myuros	0	0·00	1·00	0	−2·80	0·35	0	−1·43	0·60	4	13·59	0·02
Westringia rigida	12	13·06	<0·01	3	−2·02	0·02	3	−0·94	0·15	5	−0·53	0·20
Zygophyllum apiculatum	11	2·17	<0·01	42	3·94	<0·01	1	−11·85	<0·01	3	−6·33	<0·01

for a stand whose membership of one or other association is uncertain, and which contains species regarded as characteristic of each. How is one to combine the data for the various species in order to decide in which association it is most appropriate to include this stand? The method of discriminant functions enables this question to be answered more precisely than the method depending on indicator value indices which was outlined in the previous section.

If measurements (say, quantities of different species) x_1, x_2, x_3 . . . are available, the discriminant function

$$X = \lambda_1 x_1 + \lambda_2 x_2 + \lambda_3 x_3 + \ldots .$$

has such values of λ_1, λ_2, λ_3 . . . . as minimize the misclassification of any stand when X is used as the means of discrimination. The method of calculation of λ_1, λ_2, λ_3 . . . . has been described by Mather (1943).

The use of this method will be illustrated on Adriani's (1945) data for Artemisietum maritimae and Puccinellietum maritimae. Three species are regarded as characteristic of the former, one of the latter (if *Obione pedunculata*, occurring only once, be ignored) and only these four species have been taken into account. In the first instance, the percentage cover has been considered, the abundance grades in Adriani's table being converted into cover in the way recommended by Braun-Blanquet (1946). The discriminant function is

$$X = 0.00427x_1 - 0.00227x_2 + 0.00242x_3 - 0.00354x_4,$$

where x_1 is the angular transform of the percentage cover by *Obione portulacoides*,
x_2 is the angular transform of the percentage cover by *Statice limonium*,
x_3 is the angular transform of the percentage cover by *Artemisia maritima*,
} "characteristic" of Artemisietum maritimae

x_4 is the angular transform of the percentage cover by *Puccinellia maritima* Parl. "characteristic" of Puccinellietum maritimae.

An analysis of variance of X in the two associations gives:

TABLE 7

ANALYSIS OF VARIANCE OF DISCRIMINANT FUNCTION BASED ON COVER BY FOUR SPECIES IN ARTEMISIETUM MARITIMAE AND PUCCINELLIETUM MARITIMAE

Data of Adriani (1945)

	Degrees of Freedom	Sum of Squares	Mean Square	F	P
Between associations . .	4	0·6920	0·1730	28·9	<0·001
Within associations . .	41	0·2453	0·0060		

The mean value of the function for the two associations is -0.0227; hence a stand whose status is uncertain would be allotted to the Artemisietum maritimae when the value found for the function was above this mean, to the

Puccinellietum maritimae when it fell below it. If this were used as the sole basis of classification 6 per cent. of the stands would be misclassified.

The smallest contribution to the discriminator is that of *Statice limonium.* If this species is omitted, the function becomes

$$X = 0.00352x_1 + 0.00268x_3 - 0.00277x_4,$$

giving a probable misclassification of 7 per cent. If the reduction in variance between associations due to the elimination of this species is compared with the error variance, it is found not to reach significance ($F = 3.96$, $n_1 = 1$, $n_2 = 41$, $P > 0.05$). In other words, *Statice limonium* does not contribute significantly to the discrimination of these two associations, and may be discarded. It may be noted that the coefficient for *Statice limonium* has the same sign as that for *Puccinellia maritima,* and that its mean percentage cover is in fact greater in the Puccinellietum maritimae than in the Artemisietum maritimae, although it is regarded as characteristic of the latter. It has already been shown that it is not significantly more constant (in Adriani's data) in this association, and this may be read in conjunction with the fact that its status in the literature is uncertain. Although Vlieger (1938), like Adriani, included it among the characteristic species of the Artemisietum maritimae, Weevers (1940) reversed the position, and regarded it as characteristic of the Puccinellietum maritimae.

The ordinary technique for computing discriminant functions is not appropriate where data for presence or absence only are available. In this case, however, one may find for each possible combination of species the community in which it is most likely to arise, and hence the probable proportion of misclassification on this basis (Binet, personal communication). If, for instance, one takes again the data of Adriani for the Artemisietum maritimae and the Puccinellietum maritimae, then the combinations of the four characteristic species indicating membership of each association are as follows, where "x" represents the presence of a species and "o" its absence, the species being considered in the same order as in the discriminant function:

Artemisietum maritimae:
o o o o
o o x o
o x o o
o x x o
o x x x
x o o o
x o x o
x o x x
x x o o
x x x o
x x x x

Puccinellietum maritimae:
o o o x
o o x x
o x o x
x o o x
x x o x

On this basis, the probability of misclassification is 2 per cent. However, *Artemisia* and *Puccinellia* alone give almost as good an indication, as follows:

Artemisietum maritimae:
. . o o
. . x o
. . x x

Puccinellietum maritimae:
. . o x

with an expected misclassification of 5 per cent.

If now, armed with these criteria, one returns to Adriani's data for individual stands, one finds discrepancies in the position of eight out of the 46 stands, as shown in Table 8.

TABLE 8

STANDS OF TWO ASSOCIATIONS WHOSE CLASSIFICATION IS CALLED IN QUESTION BY OBJECTIVE CRITERIA

Data of Adriani (1945)

Association	Stand	Criterion			
		Presence of Two Species	Presence of Four Species	Cover by Three Species X	Cover by Four Species X
Artemisietum	4			−0·0126	−0·0799
	6	o x	x x o x		−0·0382
	7	o x	x x o x		
	9	o x	o x o x	−0·0050	−0·0627
Puccinellietum	6			+0·0186	
	8			+0·0186	
	9			+0·0186	
	17	x x	x x x x		

It will be noted that one of these stands, although put by Adriani in the Artemisietum, would be transferred to the Puccinellietum by any of the four criteria adopted. Three other stands would be transferred on the "presence" criteria, and four others on one or both of the "cover" criteria. The fact that the criteria have themselves been based on data including these particular stands would lead one to expect the criteria to be biased in favour of allotting them to the particular communities in which Adriani included them. The large number of discrepancies is thus all the more noteworthy; it suggests that either Adriani's classification was at fault in some cases, or that in classifying the stands he was relying on data not made explicit in his paper.

The same methods can, of course, be applied in the allocation of associations to higher classificatory units as well as in the allocation of stands to associations. Such a question has been discussed by Drees (1949) in one of the few papers applying tests of significance to results obtained by the methods of the Zürich-Montpellier school. The Linarietum spuriae of Kruseman and Vlieger (1939) contained species characteristic of the Rudereto-Secalinetalia, and others characteristic of the Chenopodietalia. Drees determined the number of species in each group occurring in each of the eight sample areas, and applied a t test to show that the mean difference in favour of the Secalinetalia was not significant. The method of discriminant functions could also have been applied to this question, with the advantage that the various characteristic species would have been given weight depending on their fidelity, instead of equal weight as was the case with Drees's method. The number of characteristic species was, however, so large that the calculations would have been very tedious.

Where discrimination between more than two communities is in question, the problem becomes more complicated. If the communities form a sequence, a single discriminant function may be enough to distinguish them and will serve to allot any given stand between them. More commonly it will not be sufficient —or at least will not make the best use of the data available. Geometrically, the problem may be interpreted as the allocation of a point in multidimensional space to one of several clusters or centres around which points are distributed. If the centres lie on a straight line, then a single function uses the data fully; otherwise, it may be necessary to fit further functions representing directions at right angles to the first until the distribution of the centres is adequately represented on the new coordinate system.

Such a situation is presented by the communities ("groupings") identified in the Victorian Mallee (Goodall 1953). The small *Cassia* grouping may be ignored from this point of view, and attention may be directed to the other three—the *Bassia*, *Vittadinia*, and *Dodonaea* groupings. On the basis of the spatial and floristic relations, the suggestion was put forward that the *Vittadinia* grouping was in some ways intermediate between the *Bassia* and *Dodonaea* groupings. The use of discriminant functions enables this hypothesis to be tested.

Table 9

MEAN PERCENTAGE COVER BY FOUR SPECIES IN THREE COMMUNITIES

Species	*Bassia* Grouping	*Vittadinia* Grouping	*Dodonaea* Grouping
Dodonaea bursariifolia . .	0·405	1·747	5·223
Melaleuca uncinata	0·144	12·596	8·848
Vittadinia triloba	0·371	0·402	0·023
Zygophyllum apiculatum . .	0·121	0·005	0·003

For the purpose of this test, species used in the separation of the groupings were ignored, and the computations were based on the four species next most frequent in the whole data—viz., *Dodonaea bursariifolia, Melaleuca uncinata, Vittadinia triloba*, and *Zygophyllum apiculatum*. The percentage of ground covered by the foliage of these species, after transformation, was used as the variable. The mean percentages in the three groupings are shown in Table 9.

The method of testing the collinearity of three such samples has been outlined by Fisher (1938). It results in an analysis of variance in which the variance between communities or groupings is divided into a collinear and a non-collinear portion, each of which may be tested against the error variance between different stands within the same community by the variance ratio (F test). In the present case, the analysis of variance reads as in Table 10.

A single discriminant function thus by no means accounts for the whole of the variance between communities, and the *Vittadinia* grouping cannot be regarded simply as intermediate between the two others.

TABLE 10

ANALYSIS OF VARIANCE, DISCRIMINATION BETWEEN THREE COMMUNITIES BASED ON PERCENTAGE COVER BY FOUR SPECIES

	Degrees of Freedom	Sum of Squares	Mean Square	F	P
Collinear discrimination	5	0·5841	0·1168	25·4	<0·001
Non-collinear discrimination	3	0·3573	0·1191	25·9	<0·001
Error	230	1·0586	0·0046	—	—
Total	238	2·0000	—	—	—

The two discriminant functions corresponding to the two portions into which the variance between communities has been divided are:

$$X = -0.00681x_1 + 0.00083x_2 + 0.00550x_3 + 0.02234x_4$$
$$Y = +0.00698x_1 - 0.00351x_2 - 0.00779x_3 + 0.00357x_4,$$

where x_1, x_2, x_3, x_4 are the transformed values for percentage cover for the four species taken in alphabetical order. The mean values for the two functions in each community are shown in Table 11.

TABLE 11

MEAN VALUES OF DISCRIMINANT FUNCTIONS IN THREE COMMUNITIES

	Function	
	X	Y
Bassia grouping	+0·0250	+0·0021
Vittadinia grouping	−0·0103	−0·0308
Dodonaea grouping	−0·0575	+0·0275

In Figure 1 are represented the positions of the means of the three communities in relation to the two rectangular axes provided by the discriminant functions. The mean for the small *Cassia* grouping has been plotted also; it occupies a more extreme position than any of the three main communities, being displaced outwards along the X-axis from the *Bassia* grouping. This accords with the view expressed earlier that it could be regarded as a more extreme variant of the latter community.

When more than one discriminant function has been computed, the allocation of any particular quadrat or stand will be slightly more complicated than for a single function. The values of the functions for the quadrat are first calculated. These values then represent a point in the new coordinate system, and the distances of this point from the means for the various communities may be determined either graphically or by the ordinary methods of coordinate geometry. The community to whose mean the new point is nearest is that to which the quadrat should be allotted.

The displacement of the *Vittadinia* grouping from the line joining the other communities, though it implies that the former is not floristically intermediate between the *Bassia* and *Dodonaea* groupings, is not inconsistent with the view that it may be intermediate in the strictly ecological sense. Only if the amount of each species present were a regularly increasing or decreasing function of each habitat factor would it be necessary to conclude that it is not intermediate in the ecological sense either. It might well be that the soil texture, say, in the *Vittadinia* grouping was intermediate between those for the *Bassia* and *Dodonaea* groupings, but that whereas the optima of this factor for *Dodonaea bursariifolia* and *Zygophyllum apiculatum* occurred at either end of the range, those for *Melaleuca uncinata* and *Vittadinia triloba* occurred near the middle, and the amount of these two species decreased towards the extremes. On the other hand, the *X*- and *Y*-axes of Figure 1 may represent two distinct ecological factors as well as the floristic elements on which they were based. Vegetational studies alone would not give an answer to this question.

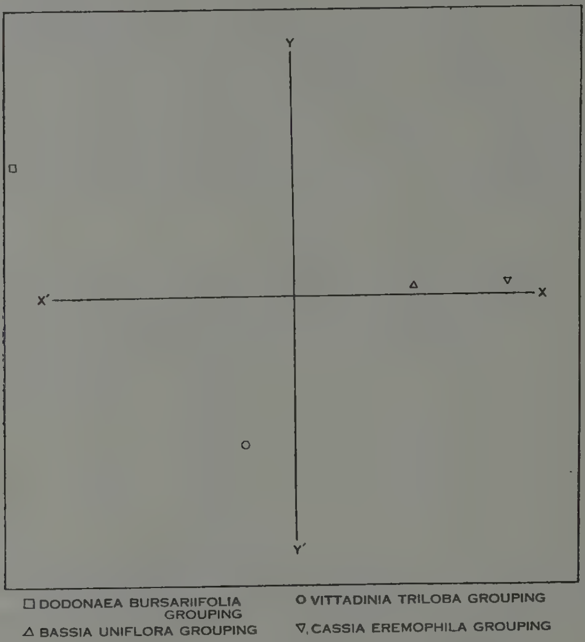

Fig. 1.—Positions of community means in relation to coordinate system provided by two discriminant functions based on angular transform of percentage cover by four species.

V. Discussion

The three main sections of this paper each deal with a different method of using data on the species present to define the sociological position of a quadrat or stand; the three methods represent, in a sense, increasing levels of generalization. The concept of fidelity is concerned only with the value of data for a single species in indicating membership of a particular community as against all others, and does not take formal account of the fact that a species may be a valuable indicator of a number of communities without being characteristic of any; this possibility is covered by the concept of indicator value, which includes that of fidelity as its more extreme instance. But determinations of fidelity and indicator value do not give precise guidance as to how information about a number of species should be combined. For this purpose, a discriminant function is required; the discriminant function contains the information from fidelity and indicator-value determinations which is relevant to the assignment of a quadrat or stand to its proper community, and in addition combines them appropriately. The discriminant function is thus a more synthetic and a more generally valid approach to the question of using data on species present to allot stands or quadrats to plant communities.

In this type of study, false or unwarranted conclusions may be reached, or labour may be wasted, if tests of significance are not applied. The fact that *Bassia parviflora*, say, is most frequent in the *Bassia uniflora* grouping (Table 5) is hardly worth even mentioning, and certainly does not justify calling *Bassia parviflora* a characteristic species of this community, when the difference in frequency is so far from significance. Another such set of quadrats may show no such difference at all. Rather few of the infrequent species are significant either in fidelity or in indicator value—and this is generally to be expected. Only if an infrequent species is highly characteristic (or has high indicator value) will the difference in frequency be significant; and unless it reaches or approaches significance the difference is hardly worth a second thought. It is true that, for instance, *Gahnia lanigera* and *Helichrysum catadromum* occur only in the *Dodonaea bursariifolia* grouping; but they were recorded only once and twice respectively in the 256 quadrats studied, and the hypothesis that they are, in fact, equally frequent in all four communities cannot be discarded with assurance; they therefore cannot be regarded as characteristic of this community until more confirmatory data have been collected.

In the case of discriminant functions, tests of the effects of omitting data for one species on the variance between communities play the same part as the significance tests for fidelity and indicator value.* But the test involves considerable computing effort, and is probably worth performing only in special circumstances; the inclusion of data for species whose contribution to the discrimination is not significant will rarely mislead.

The use of random quadrats is not a necessary prerequisite to the application of the indices of fidelity or indicator value proposed here, or to the computation of discriminant functions; that has been shown by the use here of data published by the Zürich-Montpellier school. But, as always with selected data, the conclusions drawn are bound to be in doubt when one wishes to extend them from the actual data recorded to the vegetation as it occurs in the field. Consequently, random quadrats are much to be preferred. It has been contended that, if quadrats are placed at random, some—perhaps many—will not be samples of homogeneous vegetation. *But vegetation is not homogeneous.* In most places, the areas over which the composition of the vegetation varies continuously from point to point considerably exceed those over which it remains constant (if indeed the latter exist). To confine one's sampling to reasonably homogeneous areas certainly simplifies problems of classification—but only at the expense of Procrustean distortion. Yet even those ecologists who believe that only homogeneous vegetation is worth classification could still, if they wished, sample at random within this limitation; their results would then be representative of the whole of the homogeneous vegetation instead merely of their own subjective selection from it. But not only should their sampling within the homogeneous areas be random; they should also apply objective criteria of homogeneity—a problem of some difficulty (see Goodall 1952, 1953)—and sample at random within *all* homogeneous areas identified.

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* If the effect on the variance is non-significant, it may be assumed that the species is without indicator value, and does not contribute to the discrimination.

The practice of amplifying detailed records on limited sample areas with general visual observations over a much wider field sometimes presents difficulties for the reader—particularly where conclusions are based on both jointly, without indication of the contribution from each source. This is generally the case with the classifications and characteristic species of the Zürich-Montpellier school. It has been shown that, in some of their recent publications, the sample areas studied (even though selected) do not support the conclusions. It seems likely that the conclusions are based on general visual observations rather than on the areas studied in detail. This throws rather a heavy strain on the reader's faith. He will probably not question the author's integrity. But he may well have doubts as to the author's ability to take full account of the variability of the vegetation, and to carry out the subjective equivalent of the significance test which he would prefer to see explicitly presented. General visual observation has its place, and an important one, in descriptive plant sociology; species highly characteristic of a particular community may be so uncommon that it would be impracticable to demonstrate them as such by random sampling, yet the experienced field worker may be well aware of their status. Such observations should certainly be recorded; but their dependence on subjective experience rather than objective tests should be made clear.

Throughout this paper it has been assumed that the plant communities are established concepts, discrete entities, and that the problem is not to establish their existence or define them, but simply to allot an arbitrary piece of vegetation to one of them, or to assess the extent to which a species is characteristic of a community. It is clear, however, that with a little modification the method of discriminant analysis could be applied without first separating the quadrats or stands into communities. The new axes (discriminate functions) fitted in the multicoordinate system could be those removing the maximum variance between individual quadrats or stands rather than between community means. In this modified form, the study would become factor analysis. The application of this technique will be the subject of a later paper in this series.

VI. Acknowledgments

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POINT QUADRAT METHODS FOR THE ANALYSIS OF VEGETATION

THE TREATMENT OF DATA FOR TUSSOCK GRASSES

By D. W. GOODALL*

[*Manuscript received August* 20, 1952]

Summary

An improved estimate of the mean cover repetition in the centres of tussocks may be obtained by fitting a negative binomial distribution by successive approximation.

I. INTRODUCTION

In a recent discussion of the use of point quadrat methods (Goodall 1952), attention was drawn to the impossibility of counting contacts with a vertical pin in the centre of grass tussocks. It was shown that, in species whose habit permits accurate counting of contacts, the relationship between the mean number of contacts ("cover repetition") and the number of points at which a (specified) small number of contacts occurred was sufficiently close to make possible a rough estimation of mean cover repetition without actually counting the contacts where they were numerous. On the assumption that the same relationship held for species growing in tussocks, it was possible to obtain an average figure for cover repetition in the centre of a tussock from the numbers of contacts recorded on their periphery. It was, however, recognized that the very difference in habit which led to this special difficulty with tussock-forming species might also mean that the relationship found for other species did not apply to them.

In the examination of data for some experimental plots on the Bogong High Plains, Victoria (Turner and Fawcett, unpublished data), the question acquired too great an importance to be dealt with in this casual fashion. In some areas, well over half the vegetation might consist of *Poa caespitosa* G. Forst. (particularly the "fine grass" variety), and at 10 per cent. of the points studied the pin might fall in the centre of a tussock. Clearly, the number of contacts allotted to *P. caespitosa* at these points could greatly affect the percentage composition of the sward as estimated from the point quadrat data. Since the observation of changes in the composition of the sward over a long period of years was a principal purpose of the study, improvement of the method of dealing with these points was clearly sufficiently important to justify further investigation.

It was shown (Goodall 1952) that in all species studied, including one variety of *Poa caespitosa,* the data for numbers of points at which different numbers of contacts were observed could be fitted by a negative binomial dis-

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* Botany Department, University of Melbourne. Present address: University College of the Gold Coast, Achimota, Gold Coast.

tribution, provided the number of points where the species did not occur was ignored. This fact provided a possible approach to the problem presented by the tussock grasses. If a negative binomial distribution could be found giving a best fit to the limited number of classes in which counting of contacts was practicable, the area of the "tail" of this distribution would indicate the number of contacts to be ascribed to those points where counting was impracticable. Even for negative binomial distributions fitted without knowledge of the zero class, no direct method of fitting was available and it was necessary to proceed by successive approximation. Where, as in the present case, one is also ignorant of the numbers of points in all classes beyond a certain point, and knows only their total number, the position becomes all the more difficult. The method adopted was to assume certain values for the number of points in the zero class and for the mean number of contacts in higher classes, combine them in all possible ways, and, making certain assumptions about the distribution among the higher classes, compute (by the method of moments) the negative binomial distribution corresponding with these assumptions, and compare it with the numbers of points in the classes actually observed by the χ^2 test. The distributions giving the lowest values of χ^2 were then used to improve the assumptions. Clearly, this rough-and-ready method could not be expected to give a maximum-likelihood solution; but, in the absence of a maximum-likelihood method for dealing with such fragmentary data, it was hoped to obtain an acceptable approximation.

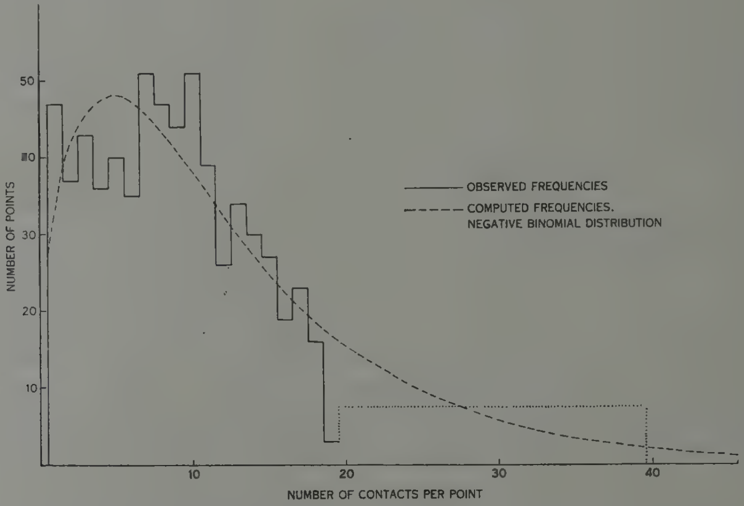

Fig. 1.—Observed and calculated distribution of numbers of contacts per point. Data for "fine grass" variety of *Poa caespitosa*, Bogong High Plains, January 1951.

II. Method of Estimation

The data for the "fine grass" variety of *Poa caespitosa* which were used in these calculations are shown in the form of a histogram in Figure 1; they were collected on the Bogong High Plains, in 1951. Observers had instructions to count contacts at each point up to 20, but to record 20 or more contacts as "x"; these records are indicated in the histogram by the final dotted column, the base of which is taken arbitrarily to cover 20 classes. The sharp decrease in numbers of records in the classes immediately below 20 gave rise to a suspicion that counts became unreliable when approaching this limit; accordingly, only records of 15 contacts or fewer were taken as trustworthy.

The form of the histogram suggested that, of the points with no contact with *Poa caespitosa,* some 40 properly formed part of the distribution; similarly, the median value for the "tail" of the distribution consisting of points with more than 15 contacts was taken as approximately 25. Accordingly, frequencies for the zero class of 20, 40, and 60, and median values for the "tail" of 20, 25, and 30 contacts were taken in all combinations for the purpose of computing negative binomial distributions. As a first approximation, the frequencies for the different classes in the "tail" was taken to be a linear function of number of contacts. These negative binomial distributions were then compared with the observed frequencies in the 15 classes regarded as trustworthy, and the resulting χ^2 values are shown in Table 1.

TABLE 1

FIRST APPROXIMATION TO FITTING OF NEGATIVE BINOMIAL DISTRIBUTION, WITH ZERO CLASS AND "TAIL" UNKNOWN. χ^2 VALUES

Median Number of Contacts in "Tail"	Frequency of Zero Class		
	20	40	60
20	85·3	62·5	54·2
25	36·9	28·9	25·0
30	21·8	22·6	23·2
35	24·7	22·8	23·9

This first series of distributions clearly indicated the need to test higher median values for the "tail" and therefore three more distributions were computed with a median value of 35, and the same frequencies for the zero class. The resulting values for χ^2 are also shown in Table 1.

It was now clear that the distribution of best fit would have parameters not widely different from those giving the value 21.8 for χ^2 in Table 1. These values were in fact $c = 0.155$, $r = 1.86$ in the expression (Greenwood and Yule 1920):

$$\left(\frac{c}{c+1}\right)^r\left\{1, \frac{r}{c+1}, \frac{r(r+1)}{2!(c+1)^2}, \quad \dots \quad \dots \quad \dots \right\}.$$

Accordingly, in the second approximation the following values were used for the parameters, in all combinations: $c = 0.13$, 0.15, 0.17; $r = 1.6$, 1.8, 2.0. The results are given in Table 2.

These values, together with those in Table 1, enabled a contour map to be drawn of the surface connecting χ^2 with the values of the parameters c and r. This contour map in turn enabled the position of the minimum to be estimated fairly precisely after a few more distributions with parameters in the neighbourhood of this minimum had been calculated. This minimum χ^2 distribution had the parameters

$$c = 0.16$$

$$r = 1.85,$$

and is illustrated by the smooth curve in Figure 1. The fit is not as close as might be hoped, for the χ^2 value (21.5) is close to that corresponding with the 5 per cent. significance level (21.0 for 12 degrees of freedom), but it seems unlikely that a much better fit could be obtained by a more precise method. The mean number of contacts in the "tail" (i.e. in all classes with more than 19 contacts) is 27.3 and this number is therefore indicated as the appropriate interpretation for points recorded as "x". In some series of observations, counting was abandoned when contacts exceeded nine, and in such cases the appropriate mean deduced from the distribution is 18.3.

TABLE 2

SECOND APPROXIMATION TO FITTING OF NEGATIVE BINOMIAL DISTRIBUTION, WITH ZERO CLASS AND "TAIL" UNKNOWN. χ^2 VALUES

r	$c = 0{\cdot}13$	$c = 0{\cdot}15$	$c = 0{\cdot}17$
1·6	22·8	28·2	44·4
1·8	35·0	22·9	25·2
2·0	75·2	36·7	23·7

If these figures are compared with those previously (Goodall 1952) derived from the general relationship between mean cover repetition and the proportion of points with few contacts, it will be appreciated that the fear then expressed that this relationship might not hold for tussock grasses was well founded. For contacts more numerous than nine per point, the mean previously used was 10—a value which, on the face of it, appeared excessively low; the corresponding value derived by the improved method, as mentioned above, is 18.3.

Tussock grasslands form important pastures in many parts of the world, and are frequently the subject of intensive investigation. It has therefore been thought worth while to publish this contribution to their analysis by point quadrat methods, though the method described would probably be too elaborate for any but intensive studies. It is clear that a considerable computational effort is required to obtain the figures presented here; such an effort would probably be worth while only where a limited area of special interest contains tussock grasses as important constituents of the vegetation.

III. ACKNOWLEDGMENT

My thanks are due to Mr. G. W. Davies for assistance with the rather tedious calculations and for preparing the diagram.

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DIFFERENCE IN MICROSPORE COMPOSITION OF SOME SAMPLES FROM A BORE AT COMAUM, SOUTH AUSTRALIA

By Isabel C. Cookson*

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Summary

The microspore content of samples from a bore at Comaum, S.A., has been determined. Evidence is brought forward which suggests that the passage from Tertiary to Mesozoic strata occurred between 620-ft and 650-ft levels. Several new sporomorphs have been described; their affinities with living and fossil types have been considered.

I. Introduction

Six samples from a bore put down by the South Australian Department of Mines at Comaum have been examined for microfossils in an attempt to determine the lower limit of the Tertiary strata in this bore.

Small quantities of each were subjected to hydrofluoric acid followed by the chlorination-acetolysis-alkali treatment of Erdtman (1943) and the residues were mounted in safranin glycerine jelly. The cores examined represent depths of 505, 567, 620, 651, 674, and 708 ft respectively. All but the two highest, a grey clay at 505 ft and a felspathic sandstone at 567 ft, contain a considerable number of pollen grains and spores but, apart from small pieces of cuticle and fragments of wood (Plate 2, Fig. 38), no other microfossils have been observed.

It has been found that the microspore content of this series is not uniform throughout, a marked change in type being observable below the level of the thin coaly layer which occurs between 619 ft 6 in. and 620 ft. In this layer pollen grains of angiosperms are well represented, those conformable with the family Proteaceae predominating, whereas in the deeper sediments, i.e. from 650 to 708 ft, although the total microspore content is relatively high, angiosperm pollen grains have not been seen. In these beds winged pollen grains of conifers are associated with spores of ferns and lycopods.

This difference in microspore composition is a direct reflection of the difference in constitution of the vegetation living at the time of the deposition of the older and younger sediments and as such suggests that floras of two distinct geological periods are represented in these samples. It is well known, as Walton (1940) has remarked, that "The Angiosperms make their appearance as a conspicuous part of the World's flora in Lower Cretaceous times" and that the types occurring then "can be referred to living families or even genera." A

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* Botany School, University of Melbourne.

certain amount of evidence is available that angiosperms were actually in existence in the preceding Jurassic period. Pollen grains comparable to those of the family Nymphaeaceae have been reported by Simpson (1937) from a Scottish Jurassic coal and Erdtman in 1948 recorded an angiosperm pollen type from Swedish Jurassic shales, but these occurrences seem to be exceptional. There appears to be little doubt, therefore, that the coal between 619 ft 6 in. and 620 ft with an angiosperm pollen content is of either Tertiary or perhaps Cretaceous age, and that the sediments from 651 ft downwards belong to the Jurassic period. This finding has its parallel in New Zealand where, from work still in progress, Couper (1951) has deduced that "there is a very distinct Triassic-Jurassic flora characterised by the absence of angiosperms and by the dominance of ferns, and fern-like plants, and gymnosperms" and that "there is an early Cretaceous to Upper Eocene flora characterised by the incoming of the angiosperms" including *Nothofagus* and Proteaceae.

II. Description of Microspores

In this paper only the more readily identifiable and conspicuous types of microspores will be considered. Some of these agree with sporomorphs from other Australian localities, others are entirely new types. The nomenclature adopted in earlier publications (Cookson 1947, 1950, 1953) has been followed here pending the establishment of definite international rules of palynological nomenclature which, it is hoped, will be the outcome of the proposed discussions to take place during the palynological congress at Paris in 1954 (Erdtman 1952).

(a) *Early Tertiary Coal at* 619 *ft* 6 *in.* (Plate 1, Figs. 1-23)

(i) *Sphagnaceae*

Sphagnites n. spt.

Fossil spores resembling those of *Sphagnum*; medium to small, tetrahedral subtriangular to almost spherical in polar view, trilete, the tetrad scar reaching or not reaching the periphery of the spore. Exospore not conspicuously ornamented.

Sphagnites australis (Cookson) comb. nov.

Trilites australis Cookson in Brit. Aust. N.Z. Antarctic Res. Exped. 1929-1931. Rep. A 2 (8): 136, figs. 58, 59, 1947.

Following is an amended description of the type: Spore tetrahedral, subtriangular in polar view, 29-39* μ, trilete tetrad scar sometimes reaching the periphery, otherwise about 8 μ long. Exospore about 2.5 μ thick, smooth or faintly patterned.

Occurrence.—Tertiary lignites, Kerguelen Archipelago.

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* New preparations have shown that the spores from which the original measurements were taken had become slightly swollen during treatment of the lignite.

Sphagnites australis forma *parva* forma nov.

Plate 1, Fig. 1

Spore subtriangular in polar view, the tetrad scar frequently reaching the periphery, 21-27 μ in diameter. Exospore smooth, about 1.5-2.5 μ thick.

Occurrence.—Abundant at this level; also occurs in the clays associated with the coal at Wensleydale, Vic.

Sphagnites australis forma *crassa* forma nov.

Plate 1, Figs. 2-4

Spore subtriangular to almost spherical, 29-36 μ in diameter, tetrad scar sometimes not reaching the periphery. Exospore smooth or slightly uneven, about 3-5 μ thick.

Occurrence.—Less frequent than S. *australis* f. *parva*. Also observed in a dark clay at the top of the coal at Benwerrin, Vic., and the clays at Wensleydale, Vic.

Comments.—Comparison with spores of only one of the three living Victorian species, *Sphagnum subsecundum* Nees, has been possible since sporocarps are only occasionally observed in Victoria (Willis 1952). The spores of S. *subsecundum* do not exactly match either of the Victorian fossil forms, being larger than S. *australis* f. *parva* and thinner-walled than S. *australis* f. *crassa*. They are tetrahedral, trilete, the diameters of acetolysed spores ranging from 28 to 35 μ, the wall is smooth, about 2 μ thick, and the tetrad scar may or may not reach the periphery.

The occurrence in European deposits of larger and smaller forms of *Sphagnum* spm. *steroides* R. Pot & Ven. is of interest. Leschik (1951) has given good figures of both types from Upper Pliocene brown coal at Buchenau (Kr. Hünfeld).

(ii) *Gleicheniaceae* (Plate 1, Figs. 5-7)

Gleichenia circinidites n. spm.

Plate 1, Figs. 5, 6

Tetrahedral, trilete, triangular in polar view, 27-40 μ in diameter, sides straight or more or less concave, according to the degree of shrinkage, slanting inwards slightly towards the angles; tetrad scar reaching the periphery. Wall about 1.5 μ, sometimes showing a delicate sculpture.

Of frequent occurrence in the Comaum coal at 619 ft 6 in.

Other occurrences.—Although fossil spores of *Gleichenia* have not previously been recorded from Australian Tertiary deposits, they have nevertheless been recognized in them. For example, they are relatively numerous in the clays and coal at Wensleydale, Vic., an early Tertiary coal at Benwerrin, Vic., and in the brown coal at Yallourn. In the Yallourn deposit it is of interest to note that pinnules of the *Gleichenia circinata* type occur at certain levels. The size range of the spores included in the sporomorph *Gleichenia circinidites* varies somewhat from one deposit to another. The range in diameters of specimens from the Yallourn coal, as is shown in Table 1, exceeds that of the examples from the type locality (Comaum coal) and approaches more nearly to that of acetolysed examples of the two living Victorian species of *Gleichenia*. The significance of this variability can only be determined by a more detailed comparative study than is possible at present.

Spores of *Gleichenia* occur throughout the Cretaceous and Tertiary deposits of New Zealand (Couper 1951, Fig. 2).

TABLE 1

DIMENSIONS OF *GLEICHENIA CIRCINIDITES*

Species	Locality	Equatorial Diameter of Spore (μ)	Approximate Thickness of Wall (μ)
Gleichenia circinidites	Comaum, S.A.	27-40	1·5
	Wensleydale, Vic.	30-37	1·5
	Benwerrin, Vic.	27-37	1·5
	Yallourn, Vic.	33-60	1·5-2·5
Gleichenia circinata	Wallaby Creek, Vic.	43-53	2·5-3
Gleichenia microphylla	Creswick, Vic.	50-60	2·5-3

(iii) *Podocarpaceae*

Coniferous pollen grains are very sparsely represented at this level. Only one type occurs frequently enough for present speciation.

Dacrydiumites mawsonii Cookson

Plate 1, Fig. 10

Several typical and well-preserved examples of this sporomorph have been isolated. In all of them the proximal tubercles which characterize this form have been prominent.

Other occurrences.—A common Tertiary type of southern Australia, Tasmania, New Zealand, and Kerguelen Archipelago.

(iv) *Fagaceae*

Nothofagus Blume

Plate 1, Figs. 11-14

Pollen grains of *Nothofagus* (Cookson 1946) are surprisingly infrequent in this deposit. The four types observed are:

Nothofagus sp. *c.* Cookson (Plate 1, Fig. 13).—This is a large type with a delicate exine thickened only around the pores.

Other occurrences include brown coals at Moorlands in South Australia and the Latrobe Valley in Victoria, and carbonaceous deposits in Tasmania and New South Wales.

Nothofagus sp. *d.* Cookson (Plate 1, Fig. 11).—A small echinate type, the exine thicker around the pores.

Other occurrences include brown coals at Moorlands, S.A., Yallourn, Vic., and Parwan, Vic.

Nothofagus sp. *e.* Cookson (Plate 1, Fig. 14).—A medium-sized angular pollen type in which the exine has a uniform thickness throughout.

Other occurrences.—Possibly the most widespread of the beech pollen types preserved in the earlier Tertiary deposits of Australia and Tasmania.

Nothofagus sp. (Plate 1, Fig. 12).—Probably a new type; it occurs, however, in insufficient numbers for present description.

(v) *Myrtaceae* (Plate 1, Figs. 15-17)

The family Myrtaceae appears to be represented in this deposit by moderate numbers of the three small pollen types illustrated in Plate 1, Figures 15 and 16. All are typically myrtaceous in their triangular form, sunken pores, and distinct arci. Further identification of these sporomorphs will not be attempted here pending the results of a comparative study of the pollen of living members of the Myrtaceae now being carried out by Miss K. Pike in the University of Melbourne.

(vi) *Proteaceae* (Plate 1, Figs. 18-23)

Triangular and typically three-pored pollen grains with variously sculptured walls, presumably attributable to the Proteaceae, are the predominant angiosperm types in the coal at 619 ft 6 in. Only a few of these are selected for consideration, the determination of the smaller types being left for the present.

Banksieidites minimus Cookson

Plate 1, Fig. 18

Small pollen grains of the *Banksia-Dryandra* type occur in moderate numbers. They are plano-convex, 32-37 μ long, 21-24 μ broad, 19-24 μ wide, with distinct apertural 'collars.' The exine is thin and the sculpture faint.

Although slightly larger than the type examples of *Banksieidites minimus* (Cookson 1950) their approximation seems sufficiently close to warrant their inclusion in this generalized sporomorph.

Other occurrences.—Brown coal at Yallourn and Yallourn North, Vic.

Proteacidites annularis Cookson

Plate 1, Fig. 19

Grains identical with the sporomorph *P. annularis* occur in small numbers. They are characterized by their small size, triangular shape in polar view, distinct apertural 'collars,' and fine sexinous reticulum.

Other occurrences.—A widely distributed Tertiary type (Cookson 1950). It has been observed in other South Australian deposits, including the brown coal at Moorlands and ligneous deposits from bores at Cootabarlow and Pidinga. Quite recently it has been isolated from ligneous beds near Denmark and Nornalup Inlet, Western Australia.

Proteacidites adenanthoides Cookson

Plate 1, Fig. 20

Pollen grains which agree with the general characters of this sporomorph are rather numerous. They are triangular in polar view with equatorial diameters of from 35 to 40 μ, and have a small-meshed sexinous reticulum which becomes finer towards the apertures.

Other occurrences.—Reported by Cookson (1950) from Cootabarlow, S.A., Wensleydale, Vic., and Vegetable Creek, N.S.W.

Proteacidites cf. *crassus* Cookson

Plate 1, Fig. 22

Rather large three-aperturate grains with equatorial diameters ranging from 36 to 51 μ, straight or concave sides, and a moderately wide-meshed reticulum, occur occasionally. They are very similar to the sporomorph *P. crassus* but are smaller than the type, and the width of the mesh seems to be the same in both hemispheres.

Other occurrences.—*P. crassus* has been recorded (Cookson 1950) from the brown coal at Moorlands and a ligneous clay from the Cootabarlow bore.

Proteacidites incurvatus Cookson

Plate 1, Fig. 21

A few examples of this sporomorph have been observed. They have equatorial diameters of from 53 to 87 μ, straight or concave sides, and the tapering incurved exine and the complicated sexinous pattern, finer towards the apertures, typical of *P. incurvatus.*

Other occurrences.—Moorlands brown coal, and the Pidinga bore in South Australia, and the clays and coal at Wensleydale, Vic.

Proteacidites granulatus n. spm.

Plate 1, Fig. 23

Grain triangular in polar view with three prominent apertural areas; sides straight, equatorial diameter 32-51 μ. Exine about 2.5 μ thick except around the apertures where it is thicker, apertural 'collars' about 5 μ deep. Sculpture fine, elements of the sexine small and crowded.

Occurrence.—Infrequent in the coaly layer at 619 ft 6 in. to 620 ft, Comaum bore, S.A.

(vii) *Pteridophyta Incertae Sedis*

Trilites gigantis n. spm.

Plate 1, Figs. 8, 9

Spore trilete, 66-104 by 52-66 μ, triangular in polar view, with rounded angles and straight to more or less concave sides (according to the degree of shrinkage); tetrad scar bordered by distinct lists, its branches reaching the angles. Wall two-layered, about 3 μ along the sides, 8-13 μ over the angles as the result of a considerable thickening of the outer layer at these points. Exospore ornamented by irregular, more or less prominently raised areas.

Occurrence.—Trilites gigantis, although relatively abundant in the Comaum coal at 619 ft 6 in., is otherwise a rare type. Apart from the Comaum occurrence it has so far only been recovered from one other Australian deposit, namely the clay parting in the lower portion of the coal at Wensleydale, Vic. Its affinity has not been determined. Mr. W. F. Harris and Mr. R. A. Couper of New Zealand have kindly informed me that they know of no New Zealand pteridophyte spore, either living or fossil, similar to *Trilites gigantis.*

(viii) *General Results*

The palynological investigation of Australian Tertiary deposits now proceeding in Melbourne has not progressed sufficiently far to permit deductions regarding the more detailed stratigraphical position of the Comaum coal to be made.

Attention may, however, be drawn to several points of agreement between the Comaum coal and the early Tertiary clay in lower part of coal seam, Wensleydale, Vic. In both deposits spores of *Sphagnum* and *Gleichenia* and pollen grains of Proteaceae are relatively numerous, while pollen grains of *Nothofagus* occur less frequently than is usual in Australian Tertiary sediments.

Sporomorphs common to both the Comaum coal and Wensleydale clay are *Sphagnites australis* f. *parva* and f. *crassa, Gleichenia circinidites, Trilites gigantis, Dacrydiumites mawsonii, Dacrydiumites florinii,** *Nothofagus* sp. *c. Nothofagus* sp. *e, Proteacidites adenanthoides, P. incurvatus, P. annularis,* and *P. granulatus.*

These facts suggest that the ecological conditions prevailing at the time of deposition were probably very similar at the two localities.

(*b*) *Pre-Tertiary Clays in the Comaum Bore*

The grey clays occurring at 651, 674, and 708 ft will be treated collectively, since differences in their microspore content lie, on the whole, in the proportion of the individual types rather than the introduction of new ones. In them spores of Pteridophyta predominate, with pollen grains of conifers in smaller numbers. No angiosperm pollen grains have been observed.

The microspore assemblage in these deposits is therefore in strong contrast to that of the coaly layer, considered above, in which angiosperm pollen grains similar to those found in Australian Tertiary strata dominate the microspore spectrum. This difference in composition suggests that the two microfloras concerned represent the vegetation of two distinct geological periods and that in the Comaum bore the passage from Tertiary to Mesozoic strata probably occurred between the 620- and 650-ft levels.

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* Cookson and Pike (1953).

The importance of microspores in Mesozoic stratigraphy has been demonstrated by Thiergart (1949) who has shown that each stage of the Central European Mesozoic has a distinctive microflora. In Australia very little attention has as yet been paid to this subject. In 1949, de Jersey figured and described microspores from a Queensland Jurassic coal and subsequently in 1951 those present in the Lower Cretaceous coal at Burrum, Queensland. The principal microspore types occurring in the Jurassic coal at Wonthaggi, Vic., were figured by Edwards, Baker, and Knight (1944) but detailed descriptions were not included. Angiosperm pollen grains are not represented in any of these deposits.

Although the microflora of the Comaum clays cannot be significantly correlated with those of other Australian Mesozoic beds owing to lack of necessary details, one interesting parallel with certain European microfloras has emerged from this investigation. It has been found that spores very similar to those of the living fern *Mohria* occur in the Comaum clays. *Mohria* is an African member of the family Schizaeaceae, with a characteristic and readily identifiable type of spore. Spores of the *Mohria* type occur in European Mesozoic and Tertiary deposits, first appearing in the Wealden (Thiergart 1949) and recuring in Paleocene, Eocene, and Oligocene beds (Thiergart 1950; Potonié 1951).

The occurrence of a similar spore type in an Australian deposit considerably extends its distribution. Spores of the *Mohria* type have not been observed in any of the recognized Australian Tertiary sediments.

(i) *Sphagnaceae* (Plate 2, Figs. 24-26)

Spores that resemble the sporomorph *Sphagnites australis* from the Comaum coal and other Victorian Tertiary deposits occur in the Comaum clays. As in the former, two varieties can be distinguished. The more numerous type (Plate 2, Fig. 24) is close to *S. australis* f. *parva*, but its wall appears to have been somewhat thinner (*c.* 1 μ) than that of the Tertiary sporomorphs; the other, which is larger and has a thicker wall, approximates more closely to *S. australis* f. *crassa*. These sporomorphs also appear to have a definite affinity with de Jersey's (1951) C_2F and $C_{12}A$ from the Burrum coal, Queensland. The sporomorph $C_{12}A$ is said to have a faintly reticulate exospore, a feature not evident in the Comaum examples.

(ii) *Lycopodiaceae*

Lycopodium austroclavatidites n. spm.

Plate 2, Fig. 35

Spore spherical to subtetrahedral; equatorial diameter 37-48 μ, tetrad scar extending to the margins. Exospore reticulate, mesh about 8-11 μ, lamellae thick, projecting beyond the periphery about 2.5 μ. The affinities of this sporomorph appear to be with members of the group of *Lycopodium clavatum* Knox (1950).

Spores of *Lycopodium* ("clavatoide type") have been recorded from European deposits by Thiergart (1950), Leschik (1951), and others.

(iii) *Schizaeaceae* (Plate 2, Figs. 29-34)

Mohrioisporites australiensis n. spm.

Plate 2, Figs. 31-34

Spore tetrahedral with rounded angles, trilete, 33-50 by 29-34 μ, tetrad scar reaching the periphery, exospore ornamented with narrow ridges which run parallel to the walls of the spore.

Occurring in clays in the Comaum bore at 651, 674, and 708 ft. Spores of this type from a second Australian locality have been isolated from a greenish grey claystone in Geol. Surv. Vic. Bore 1, Birregurra, Vic., at 10078-10079 ft. Dr. D. E. Thomas believes the age at this level to be Jurassic.

Comments.—This sporomorph closely resembles the spores recorded from European Wealden and early Tertiary deposits by Thiergart (1940, 1949) under the name *Mohria* Typus and the one figured by Potonié (1951, Plate 20, Fig. 14), under the name *Mohrioisporites dorogensis* R. Potonié & Gell. It is possible that the European and Australian forms are spores of one species. However, in view of their widely separated geographical locations and the lack of comparative material the new spormorph *Mohrioisporites australiensis* has been proposed for the Australian examples. Potonié's nomenclature has been adopted.

Lygodiosporites adriennis R. Potonié & Gell f. *mesozoicus* Thiergart

Plate 2, Figs. 27, 28

Spore tetrahedral trilete with strongly rounded angles and usually slightly concave sides; diameter 34-66 μ; wall about 2.5 μ thick, smooth, tetrad scar usually not reaching the periphery.

Comments.—*Lygodiosporites adriennis* is apparently a common spore in European Mesozoic and Early Tertiary deposits. Thiergart (1949) has described the Mesozoic types under the name '*Sporites adriennis* f. *mesozoicus*' and it is with this form that the Comaum specimens are so strikingly comparable. If the spore illustrated in Plate 2, Figure 29, of this paper is compared with the one from the Wealden illustrated by Thiergart (1949, Plate 4/5, Fig. 9) the two will be found to be identical in every respect. Moreover, the size range in the Comaum specimens approximates closely to that of the European examples.

Recently Potonié, in dealing with European Tertiary occurrences of '*Sporites adriennis*,' substituted the name *Lygodiosporites adriennis*, thereby inferring a definite affinity with the schizaeaceous fern *Lygodium*, and this name has been adopted for the Australian form. The taxonomy of *Lygodiosporites adriennis* has been discussed by Kräusel and Weyland (1951) and need not be entered into here. Doubts have been expressed as to whether this sporomorph represents a member of the family Schizaeaceae or Cyatheaceae. Kräusel and Weyland have retained it in the Schizaeaceae.

(iv) *Osmundaceae* (?)

Trilites comaumensis n. spm.

Plate 2, Figs. 27, 28

Spores more or less spherical, 29-59 μ in diameter, trilete, the tetrad scar extending to the periphery. Wall thin, rather closely ornamented with blunt rod-like processes, about 1.2 μ long.

One of the commonest sporomorphs in the Comaum clays.

Comments.—The affinity of *Trilites comaumensis* is uncertain. It resembles, to some extent, the spores of the group of *Selaginella stolonifera* (Knox 1950), but the diameters of the larger examples exceed those given by Knox for living members.

T. comaumensis also has features in common with spores of the Osmundaceae, and it seems probable that its true affinity lies with this family. A comparison of the fossil sporomorph with the spores of the two southern osmundaceous genera *Todea* and *Leptopteris* has shown that the former approximates more closely to those of *Leptopteris,* especially those of the Australian species *L. fraseri* (H. & G.) Presl. than it does to those of *Todea barbara* Moore.

Of the fossil spores referred to the Osmundaceae the Mesozoic type *Todites hartzi* Harris (1931, Plate 10, Fig. 3) is not unlike *Trilites comaumensis,* and the same may be said of the spore type cf. *Todea* of Leschik (1951, Plate 2, Fig. 7) from a Pliocene deposit at Buchenau (Kr. Hünfeld).

(v) *Pteridophyta Incertae Sedis*

Trilites truncatus n. spm.

Plate 2, Fig. 36

Spore tetrahedral, trilete, subtriangular in polar view, about 31-55 μ in diameter; exospore ornamented with coarse, evenly spaced truncate processes about 3.5 μ long, tetrad scar reaching the periphery. A rare type; affinity undetermined.

(vi) *Gymnosperms*

Podocarpaceae (Plate 2, Figs. 39-42).—Two- and three-winged pollen grains, which probably represent the family Podocarpaceae, occur in the clays from 651 to 708 ft. They are frequently unexpanded, crumpled, or unfavourably exposed. Typical examples have been selected for illustration, but no attempt has been made to relate them to either living or fossil types.

The three-winged forms vary in size, the smaller examples (Plate 2, Figs. 39, 40) are reminiscent of the sporomorph *Microcachrydites antarcticus* Cookson 1947, and examples illustrated by Edwards, Baker, and Knight (1944) from Wonthaggi coal.

Disaccites grandis n. spm.

Plate 2, Fig. 41

This is a particularly large pollen type of infrequent occurrence. The grains have overall lengths of 80-100 μ and widths of 60-78 μ, the body is about 44-47 μ across, but its outline is sometimes difficult to see; there is a clearly defined furrow. The bladders are large and extend along the whole length of the furrow. They have a small-meshed reticulum and the surface of the cap appears to be finely reticulate.

Edwards, Baker, and Knight (1944) mention still larger two-winged pollen grains from Wonthaggi coal, but there has been no opportunity of comparing this form with *Disaccites grandis.*

(vii) *Incertae Sedis*

Monosulcate pollen grains, such as occur in the Cycadales and Ginkgoales, are extremely rare in the Comaum clays. One of the few examples is shown in Plate 2, Figure 39. It is about 46 μ long and the exine appears to be faintly roughened. Edwards, Baker, and Knight (1944) recorded 'boat shaped' microspores from the Jurassic coal at Wonthaggi.

III. ACKNOWLEDGMENTS

I wish to thank Mr. S. B. Dickinson, Director of Mines, South Australia, for entrusting the geological specimens to me for examination; Dr. A. B. Edwards, C.S.I.R.O., Melbourne, and Miss K. Pike, University of Melbourne, for help in the preparation of this paper, and Mr. P. F. Morris and Mr. J. H. Willis, National Herbarium, Melbourne, Mr. D. Ashton, University of Melbourne, and Mr. W. Litster, Victorian School of Forestry, Creswick, for living material.

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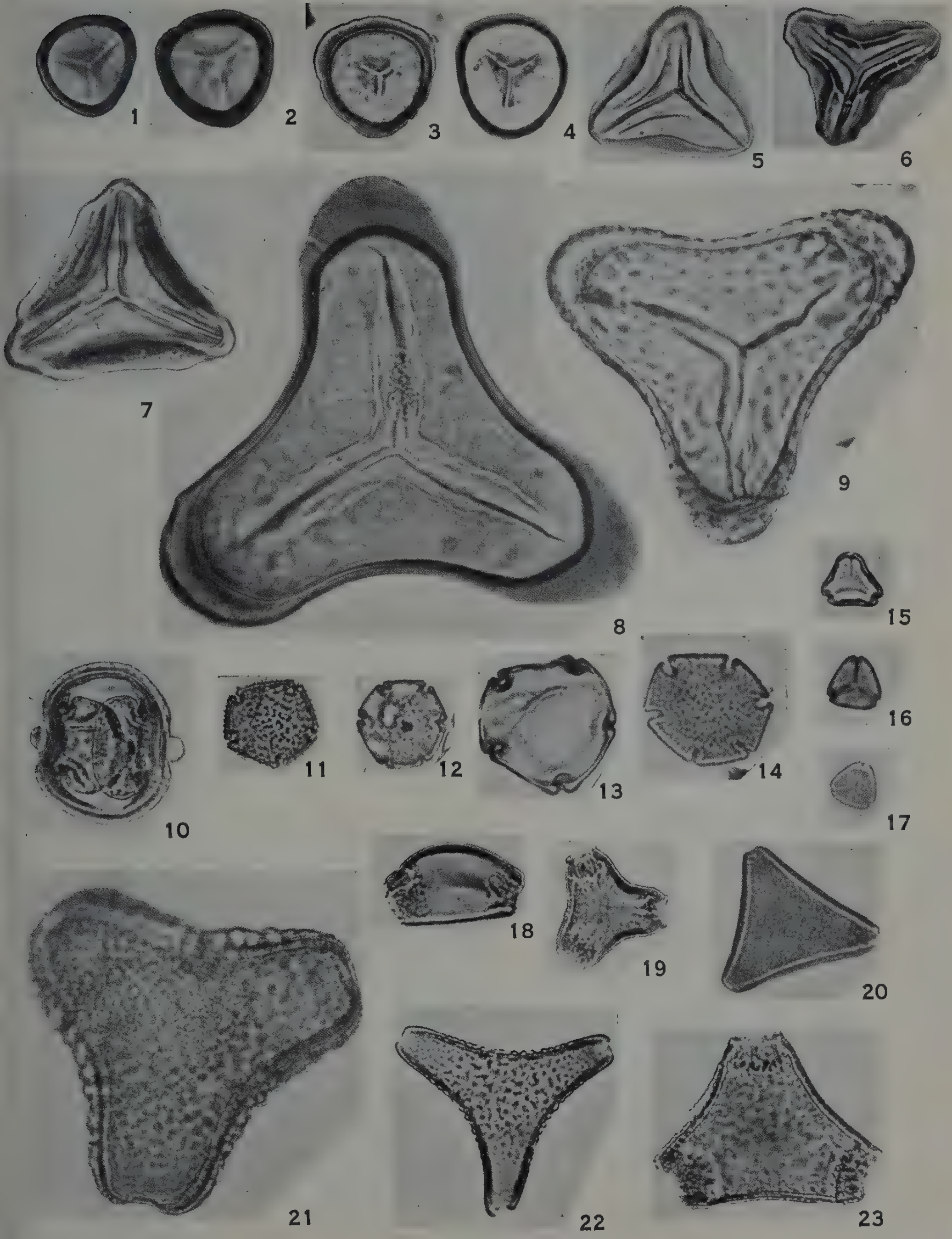
MICROSPORES FROM COMAUM, S.A.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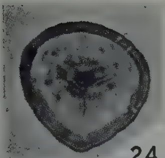
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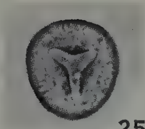
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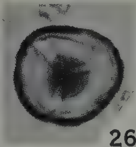
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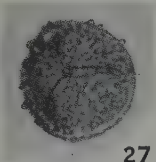
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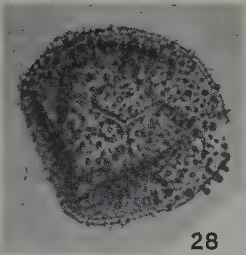
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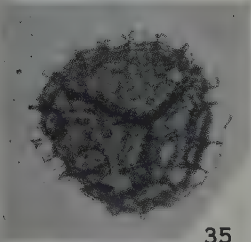
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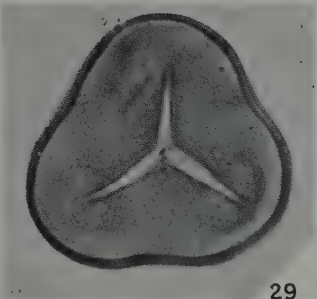
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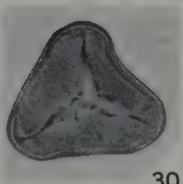
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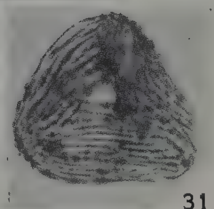
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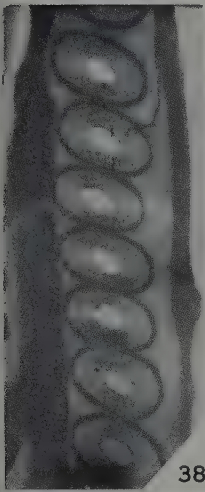
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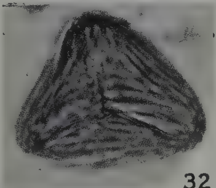
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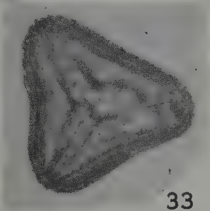
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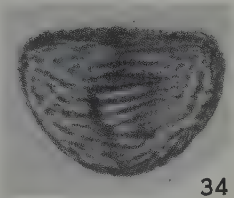
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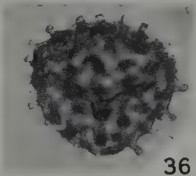
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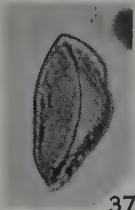
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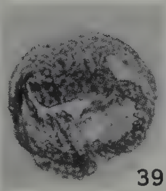
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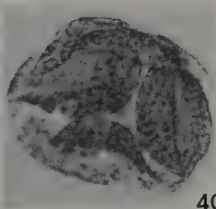
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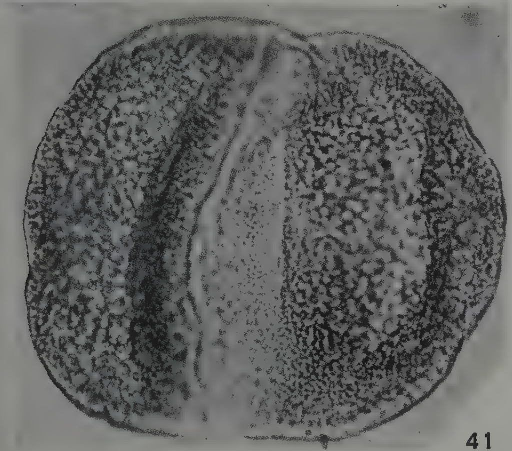
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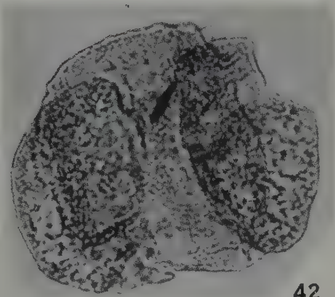
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EXPLANATION OF PLATES 1 AND 2

All the photographs are from untouched negatives; all were taken at a magnification of 600 diameters.

PLATE 1

Spores and pollen grains from the coal in the Comaum Bore at 619 ft 6 in.

Fig. 1.—*Sphagnites australis* f. *parva* f. nov.
Figs. 2-4.—*Sphagnites australis* f. *crassa* f. nov.
Figs. 5-6.—*Gleichenia circinidites* n. spm.
Fig. 7.—*Gleichenia circinata,* Wallaby Creek, Vic.
Figs. 8-9.—*Trilites gigantis* n. spm.
Fig. 10.—*Dacrydium mawsonii.*
Fig. 11.—*Nothofagus* sp. *d.*
Fig. 12.—*Nothofagus* sp.
Fig. 13.—*Nothofagus* sp. *c.*
Fig. 14.—*Nothofagus* sp. *e.*
Figs. 15-17.—Pollen grains probably referable to the family Myrtaceae.
Fig. 18.—*Banksieidites minimus.*
Fig. 19.—*Proteacidites annularis.*
Fig. 20.—*Proteacidites adenanthoides.*
Fig. 21.—*Proteacidites incurvatus.*
Fig. 22.—*Proteacidites* cf. *crassus.*
Fig. 23.—*Proteacidites granulatus.*

PLATE 2

Spores and pollen grains in clays from the Comaum Bore between 651 and 708 ft.

Fig. 24.—Cf. *Sphagnites australis* f. *crassa.*
Figs. 25-26.—Cf. *Sphagnites australis* f. *parva.*
Figs. 27-28.—*Trilites comaumensis* n. spm.
Figs. 29-30.—*Lygodiosporites adriennis* Pot. & Gell f. *mesozoicus* Thiergart.
Figs. 31-34.—*Mohriosporites australiensis* n. spm.
Fig. 35.—*Lycopodium austroclavatidites* n. spm.
Fig. 36.—*Trilites truncatus* n. spm.
Fig. 37.—A monosulcate pollen grain.
Fig. 38.—Portion of a tracheid comformable with those of the family Podocarpaceae.
Figs. 39-40.—Three-winged pollen grains of Podocarpaceae.
Fig. 41.—*Disaccites grandis* n. spm.
Fig. 42.—A two-winged podocarpaceous pollen grain.

A CONTRIBUTION TO THE TERTIARY OCCURRENCE OF THE GENUS *DACRYDIUM* IN THE AUSTRALIAN REGION

By Isabel C. Cookson* and Kathleen M. Pike*

[*Manuscript received November* 21, 1952]

Summary

Foliage shoots and seeds of a new Tertiary species, *Dacrydium rhomboideum*, are described; the affinity of *D. rhomboideum* is discussed.

A new sporomorph, *Dacrydiumites florinii*, is proposed for fossil pollen grains, similar to those of certain species of *Dacrydium*, isolated from Tertiary deposits in Australia, Tasmania, and New Guinea.

Descriptions of the pollen grains of the living species *Dacrydium araucarioides* and *Dacrydium balansae* are included.

I. Introduction

Only two of the living species of the genus *Dacrydium* are found at present in the Australian region, that is, the area comprising New Guinea, Australia, and Tasmania. One of these, *Dacrydium franklinii* Hook. f., is restricted to Tasmania, the other, *D. novoguineënse* Gibbs, to New Guinea. *Dacrydium* is not represented in the present Australian mainland flora.

Until lately nothing certain was known about the past occurrence of *Dacrydium* in this area. *Dacrydium cupressinoides* Ett. may, as Florin (1940) has stated, "represent a species of *Dacrydium* (cf. *D. balansae* Brong. et Gris. of New Caledonia)," but there is no proof that such was the case.

Recently, however, Cookson (1953) has been able to show, from the occurrence in Australian Tertiary deposits of pollen grains morphologically identical with those of *Dacrydium franklinii*, that a species of *Dacrydium* closely allied to *D. franklinii* was widespread in the southern half of Australia during the early Tertiary period.

In the present paper clear proof of the contemporaneous existence in the Australian region of a second species of *Dacrydium* will be presented. This has been derived from the study of fossil shoots, seeds, and pollen grains which are conformable with those of certain living species of *Dacrydium*. The shoots and seeds were collected from the Victorian brown coal deposit at Yallourn; the pollen grains were isolated from Tertiary deposits of various horizons in New Guinea, Australia, and Tasmania.

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* Botany Department, University of Melbourne.

II. DACRYDIUM RHOMBOIDEUM sp. nov.

Plate 1, Figs. 1-10; Plate 2, Figs. 10-14, 16, 19

(*a*) *Foliage Shoots*

(i) *External Characters* (Plate 1, Figs. 1-3)

The specimens are small, usually unbranched, slender, leafy axes, about 1.5-2 mm wide. The leaves, 1-1.5 mm long, are closely and spirally arranged; they are rhomboidal, keeled on the lower surface, appressed, slightly decurrent, and narrow towards a pointed apex.

(ii) *Cuticular Structure of the Leaves* (Plate 1, Figs. 5-7; Plate 2, Figs. 10, 11)

Lower epidermis (Plate 1, Fig. 7; Plate 2, Fig. 11).—The leaves are amphistomatic. The stomata, which are arranged in longitudinal rows, are restricted to 2 triangular areas that extend from the base to a short distance below the apex of the leaf. The stomatal rows are most numerous in the region of the pulvinus where they number from 4 to 6. There are 3 stomata-free areas, a wide central one and 2 narrower lateral ones.

The stomata are longitudinally oriented; they are amphicyclic but the polar encircling cells are often absent. The guard cells are surrounded by from 4 to 6 subsidiary cells, 2 of which are always polar; frequently 2 stomatal groups have a polar subsidiary cell in common. The radial walls of the subsidiary cells are pitted and more or less straight, those of the encircling cells being more strongly pitted and straight or slightly undulate.

The epidermal cells are rectangular with the longer diameter parallel to the length of the leaf and arranged in regular longitudinal rows; their lateral walls are thick, strongly pitted, and undulate. The epidermal cells of the central area have somewhat thicker walls than those of the stomatal and lateral stomata-free zones.

Upper epidermis (Plate 2, Fig. 10).—The stomatal groups are fewer than on the lower epidermis. They occur in short, sometimes broken longitudinal rows and their number varies with the size of the leaf.

The epidermal cells are rectangular with thick, straight, pitted lateral walls. They are somewhat larger and have less strongly pitted lateral walls than those of the lower surface.

Margin (Plate 1, Figs. 5, 6).—The epidermal cells at the junction of the 2 surfaces are ctenoidally arranged, becoming more pronouncedly so towards and at the apex.

(iii) *Internal Anatomy* (Plate 1, Figs. 4, 8, 9)

Leaves.—The epidermal cells are square in transverse section. Their outer walls are thick (about 10.5 μ on the lower surface, and 5 μ on the upper surface) and highly cutinized; several cryptocrystalline layers are evident. Beneath the epidermis on both surfaces is a well-developed hypodermis composed of from 1 to 3 layers of fibres, broken only at the stomata. The guard cells are depressed and lie obliquely to the surface; they are overarched by prominent papilla-like outgrowths of the subsidiary cells; the encircling cells are indistinguishable from ordinary epidermal cells. The mesophyll is composed mainly of palisade parenchyma. There is a single resin canal below the vascular bundle but the details of the bundle are not clear. Transfusion tissue has not been distinguished.

Stem.—A well-marked zone of radially arranged tracheids surrounds a small pith. A ring of resin canals occurs in the cortex (Plate 1, Fig. 4).

(iv) *Occurrence*

The foliage shoots of *Dacrydium rhomboideum* were collected in November 1949, from No. 1 Dredge face (east side), Yallourn Open Cut, Vic. The age of the deposits is generally accepted as Oligocene.

(v) *Comparison of* D. rhomboideum *with Living and Fossil Species*

Living species.—Several conifers still living in Tasmania, New Zealand, and New Caledonia have leaves morphologically similar to those of the fossil *D. rhomboideum.* These include *Microcachrys tetragona* Hook., *Pherosphaera hookeriana** Arch., *Athrotaxis cupressoides* Don, *Diselma archeri* Hook. f., and several species of *Dacrydium.* However, *D. rhomboideum* with a spiral phyllotaxis can be readily separated from *Microcachrys* and *Diselma,* in which the leaves are decussately arranged, and from *Pherosphaera hookeriana* and *Athrotaxis cupressoides* by certain constant cuticular features.

The reference of the fossil shoots to *Dacrydium* is supported by their agreement as regards cuticular structure and internal anatomy with living species of this genus.

Florin (1931) has arranged the recent species of *Dacrydium* in three groups, *A. B,* and *C,* largely on the basis of epidermal characters. Species group *A* comprises *D. falciforme* Pilg. and *D. taxoides* Brong. & Gris.; group *B, D. araucarioides* Brong. & Gris., *D. balansae* Brong. & Gris., *D. beccarii* Parl., *D. cupressinum* Sol., *D. elatum* Wall., *D. gibbsiae* Stapf., *D. lycopodioides* Brong. & Gris., and *D. novoguineëse* Gibbs.; group *C, D. bidwillii* Hook. f., *D. biforme* Pilg., *D. colensoi* Hook., *D. fonkii* Benth., *D. franklinii* Hook. f., *D. intermedium* Kirk., and *D. laxifolium* Hook. f.

Detailed comparisons of *Dacrydium rhomboideum* with the majority of the living species have shown that the fossil form has a closer affinity with the members of group *B* than with those of either group *A* or *C*. It is distinct from *D. taxoides* and *D. falciforme* in having bifacial leaves only and from the species in group *C* in having regularly arranged, rectangular epidermal cells with undulate, conspicuously pitted lateral walls rather than the polygonal epidermal cells with straight, moderately pitted walls typical of this group.

The relationship of *D. rhomboideum* to the members of group *B* on the other hand is clearly indicated by the occurrence in the former of epidermal cells with the strongly pitted, more or less undulate lateral walls characteristic of all recent members of this group. Within the group itself, however, *D.*

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* In a recent paper Garden and Johnson (1950) suggest that this plant should be known as *Microstrobos niphophilus.*

rhomboideum appears to be quite distinct from all the living species. Its leaves are relatively shorter and broader, the stomatal rows correspondingly shorter, and the stomata fewer than in these species.

Fossil species.—Dacrydium cupressinoides Ett. from Vegetable Creek, N.S.W., is the only known Australian Tertiary conifer with a possible affinity with *Dacrydium rhomboideum.* Florin (1940) has already drawn attention to the external resemblance of *D. cupressinoides* to the recent New Caledonian species *D. balansae* (group *B*) but in the absence of structural details even the generic relationship of *D. cupressinoides* is uncertain. Shoots of *D. cupressinoides* and *D. rhomboideum* can be readily distinguished from one another by the shape of their leaves.

It would be of considerable interest if the identity of *D. cupressinoides* could be determined for, as will be shown below, pollen grains similar to those of the species of *Dacrydium* comprising group *B* are relatively abundant in the Vegetable Creek deposit. This occurrence clearly demonstrates that a species of *Dacrydium* related to the recent members of group *B*, as well as to the fossil member *D. rhomboideum,* existed in the Vegetable Creek area during the Tertiary period.

The extra-Australian remains attributed to *Dacrydium* are imperfectly known. Of the New Zealand Eocene fossil *Dacrydinium cupressinum* Ett. that has been compared with the living species *Dacrydium cupressinum,* Florin (1940, p. 46) has remarked that it "may in my opinion well belong to this genus."

(*b*) *Seeds*

Several isolated seeds that have proved to be those of a species of *Dacrydium* were found at Yallourn in close association, though not in organic connection, with branchlets of *Dacrydium rhomboideum.* Although it cannot be actually proved that the seeds were specifically identical with *D. rhomboideum,* there is some evidence in favour of the view adopted here that such was probably the case.

External characters (Plate 2, Figs. 12-14).—The seeds are ovoid, sometimes slightly compressed, about 3-4 mm long and 2.3 mm broad; there is no trace of an epimatium.

Anatomical features (Plate 2, Figs. 16, 19).—The epidermal cells of the integument are rectangular to polygonal, with the longer diameter parallel to the longitudinal axis of the seed; their lateral walls are straight, unpitted, and about 3-5 μ thick. Stomata are absent. A relatively thick layer composed of numerous rows of elongated thick-walled stone cells with long, narrow pits lies beneath the epidermis (Plate 2, Fig. 19).

Affinity.—The development, in the integument of the fossil seeds, of a pronounced middle zone composed entirely of stone cells, a feature indicative of a dry state at maturity, and the absence of an epimatium, provide sound reasons for the reference of the fossil seeds to *Dacrydium* rather than to *Podocarpus,* in which the integument is fleshy and fused with the epimatium (Sahni and Mitra 1927).

Seeds of only two of the recent species of *Dacrydium*, *D. cupressinum* and *D. araucarioides*, have been available for more detailed comparisons. Both approximate in size and shape to those of the fossil seeds but whereas in the latter and those of *D. cupressinum* there is no epimatium, a small scale-like epimatium surrounds the base of the seed of *D. araucarioides*.

Comparisons of cuticles removed from the living and fossil seeds (Plate 2, Figs. 16-18) have shown that the cells of the outer layer of the integument of all three species have thick, straight, and unpitted walls; stomata have not been observed.

The possibility that the fossil seeds may have been derived from a second species of *Dacrydium*, known by its pollen grains *Dacrydiumites mawsonii* Cookson (1953) to have also existed in the Yallourn area, has to be considered. Judging by the great similarity between this sporomorph and the pollen grains of *Dacrydium franklinii* the two species must have been very closely related to one another. *D. franklinii* is a member of Florin's group *C* and as such is distinguishable by the cuticular structure of its leaves from those of *D. rhomboideum*. Furthermore, the seeds of *D. franklinii* are described by Dallimore and Jackson (1948) as "globular" and in this respect are unlike seeds of *D. rhomboideum*.

Until other species of *Dacrydium* can be shown to have occurred in the Yallourn area during the deposition of the coal, it seems reasonable to assume that the shoots and seeds referred to here as *D. rhomboideum* were isolated portions of the same species.

III. Fossil Pollen Grains of Dacrydium (Group B) from the Australian Region

(*a*) *General Considerations*

The uniformity as regards leaf morphology that exists amongst the species of *Dacrydium* comprising Florin's group *B* appears to extend also to their pollen grains since those of the five species that have been examined are of the same type. They have medium to large spherical bodies, relatively small puff- or frill-like bladders with coarse radial reticulations, and frequently inconspicuous furrows. The pollen of *D. cupressinum*, *D. elatum*, and *D. gibbsiae* has already been described by Cranwell (1942), Erdtman (1943), and Wodehouse (1935) respectively; that of *D. araucarioides* and *D. balansae* will be considered in this paper.

Pollen grains similar to those of living members of *Dacrydium* (group *B*) are of common occurrence in Australian deposits of Palaeocene (Raggatt and Crespin 1952) to Pliocene age and are also present in Papuan Pliocene coals. A considerable variation both in size and form occurs amongst them but whether, as seems probable, they represent more than one Tertiary species of *Dacrydium* (group *B*) cannot be proved. In view of the difficulty and uncertainty attending an arbitrary separation of individual pollen types from such variable material, it is proposed that fossil pollen grains of the type of *Dacrydium* (group *B*) from the Australian region should be included in one broadly specified sporomorph to be known as *Dacrydiumites florinii.*[*] This proposal is supported by the occurrence of a wide size range amongst pollen grains of *D. elatum* and the variable degree of development of the bladders in *D. cupressinum* as reported by Cranwell (1942).

(*b*) Dacrydiumites florinii *n. spm.*

Plate 3, Figs. 20-35

Body of grain more or less spherical, 23-78 μ in diameter. Bladders typically 2, sometimes 3, relatively small, free or united in a frill around the region of the furrow, the internal thickenings forming well-defined, radially arranged "loops" on the margins; sometimes reduced with indefinite outlines, or merely coarse reticulations of the distal surface. Furrow variable, frequently indistinct; triangular in 3-winged grains.

TABLE 1

RANGE IN BODY DIAMETERS OF THE SPOROMORPH *DACRYDIUMITES FLORINII* FROM SOME TERTIARY DEPOSITS IN THE AUSTRALIAN REGION

Locality	Body Diameter (μ)
New Guinea	
Shu Creek*	31-57
New South Wales	
Vegetable Creek	31-60
Victoria	
Balcombe Bay	36-78
Eastern View	34-47
Hamilton	27-36
Lal Lal	27-78
Stony Creek, Daylesford	26-52
Wensleydale*	26-59
Yallourn	34-62
South Australia	
Cootabarlow	27-58
Moorlands	27-38
Pidinga	23-62
Western Australia	
Denmark	26-44
Nornalup Inlet	30-65
Tasmania	
Ouse	39-56

*Localities at which fragments of cuticle, similar to that of *Dacrydium rhomboideum*, have been observed.

Exine of cap 2-layered, about 2-4 μ thick, finely rugulate, merging into the coarser texture of the wings.

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[*] The specific name has been given in appreciation of the work done on southern conifers by Professor R. Florin of Stockholm.

(*c*) *Distribution*

The sporomorph *Dacrydiumites florinii* occurs in most of the southern Australian Tertiary deposits (see Cookson and Pike 1953, Fig. 1) in some of which it is relatively abundant. It extends from Western Australia, where it has been found at three horizons, to the eastern portion of the continent and from Tasmania to north-eastern New South Wales. So far *Dacrydiumites florinii* cannot be reported from Queensland but the number of deposits from this State available for examination has been very small.

One of the most interesting occurrences of *D. florinii* is in coaly and carbonaceous deposits from New Guinea, an area in which a species of *Dacrydium* of group *B* still exists. Unfortunately, however, it has not been possible to obtain pollen of *Dacrydium novoguineënse* for direct comparison with the New Guinea examples of the sporomorph *Dacrydiumites florinii.*

WESTERN AUSTRALIA: Nornalup Inlet. Lignite. Geol. Dept. Univ. W. Aust. No. 32982. Age: Tertiary.

Hay-Denmark Railway, deviation at 354 miles. Carbonaceous sandy deposits from bores. Geol. Dept. Univ. W. Aust. No. 8662. Age: Tertiary.

Sample 8662/1 50 ft below surface; "coffee rock."

Sample 8662/9 from No. 9 bore.

SOUTH AUSTRALIA: Pidinga, south of Ooldea. Lignite from S. Aust. Dept. of Mines bore at 11-16, 31-36, 36-42 ft. Age: Tertiary.

Cootabarlow, east of Lake Frome. Carbonaceous shale from S. Aust. Dept. of Mines bore at 515-537 and 537-538 ft. Age: ? Early Tertiary.

Moorlands. Brown coal. Age: ? Oligocene.

VICTORIA: Stony Creek, Daylesford. Ligneous clay. Age: Middle Pliocene (Coulson 1950).

Hamilton. Carbonaceous clay from north bank of Grange Burn. Age: Upper Pliocene (Gill 1952).

Wensleydale. Clay parting in brown coal. Age: Early Tertiary. G.S.V. 50083.

Eastern View. Lignite outcropping in Coal Mine Creek, 100 yd upstream from Great Ocean Road. Age: Palaeocene to Lower Eocene (Raggatt and Crespin 1952).

Anglesea. Black carbonaceous sandstone from coastal cliff near mouth of Anglesea River. Age: ? Middle Eocene (Raggatt and Crespin 1952).

Bacchus Marsh. Brown coal from Lucifer mine. Age: ? Oligocene.

Lal Lal. Carbonaceous clay from Vic. Dept. of Mines bore 60, at 69 ft. Age: ? Oligocene.

Balcombe Bay. Mudstone containing leaf remains from coastal cliff. Age: Miocene (Singleton 1941).

Berwick. Clay underlying Older Volcanics at Wilson's Quarry. Age: Oligocene. Nat. Mus. Vic. No. P. 15680.

Yallourn. Brown coal at various horizons in the Open Cut. Age: Oligocene.

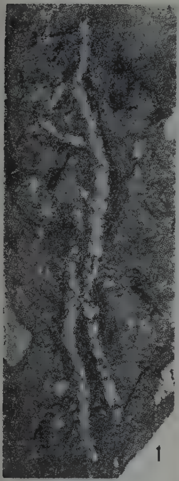
NEW SOUTH WALES: Berridale, Wullwye Creek. Ligneous clay over 100 ft below the basalt. Portion of Dr. J. Dulhunty's coal sample 89. Age: ? Early Tertiary. Nat. Mus. Vic. No. P. 15718.

Vegetable Creek (Emmaville). Mudstone from Deep Leads. Age: Oligocene (Singleton 1941). Melb. Univ. Geol. Dept. No. 890.

TASMANIA: Ouse. Lignitic seam in the Ouse River about 400 yd upstream from Bridge Hotel. Age: ? Oligocene.

Launceston. Lignite from borehole near King's Pier between 52 and 78 ft below natural surface. Age: Tertiary.

TERTIARY *DACRYDIUM* IN THE AUSTRALIAN REGION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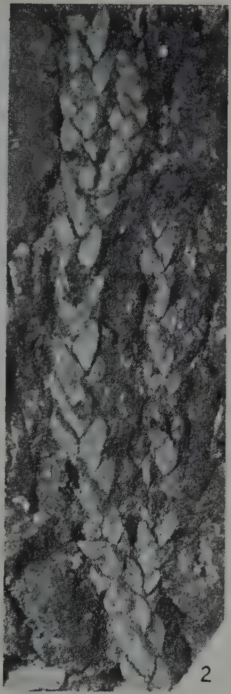
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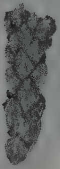
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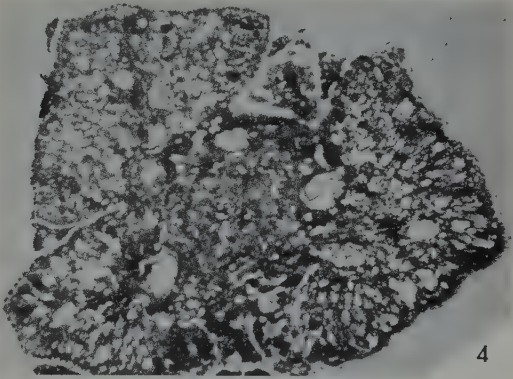
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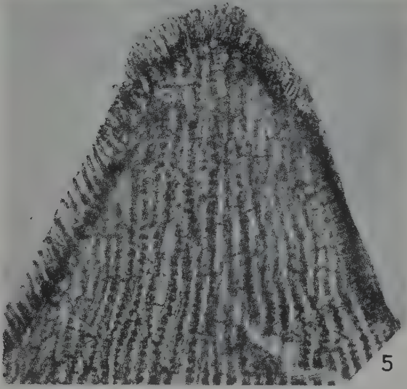
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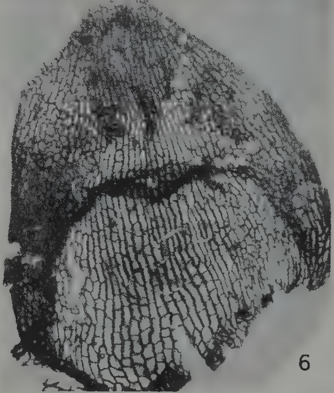
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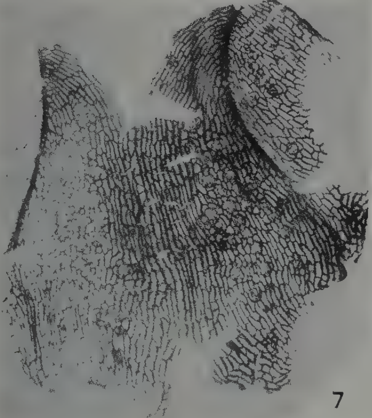
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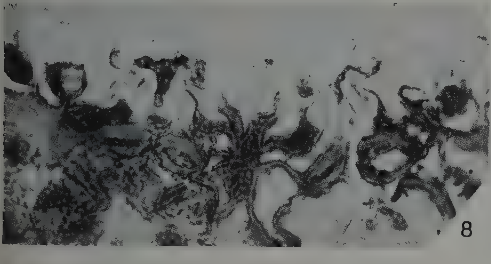
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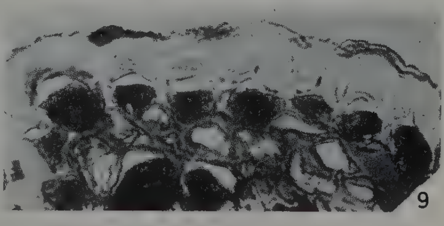
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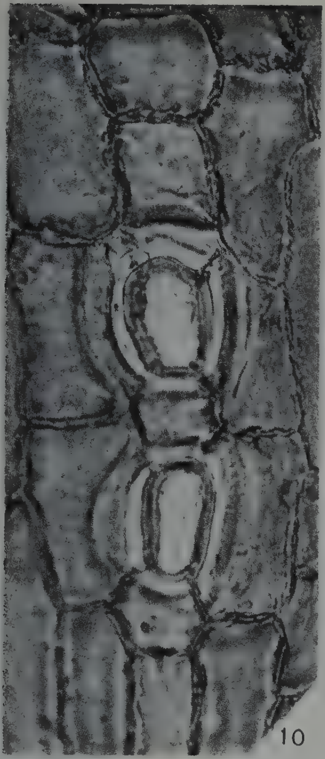
TERTIARY *DACRYDIUM* IN THE AUSTRALIAN REGION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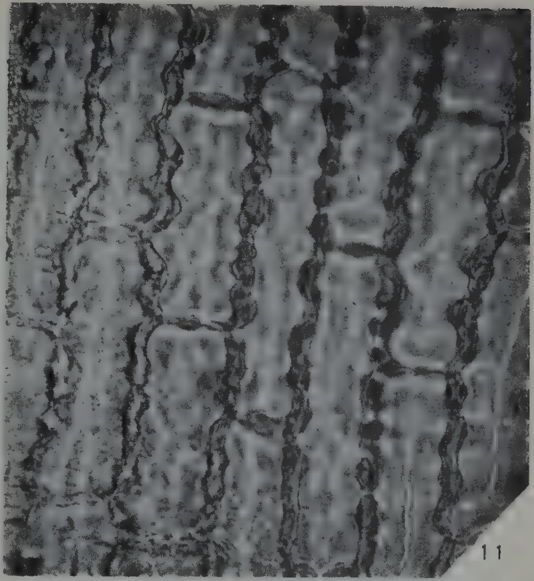
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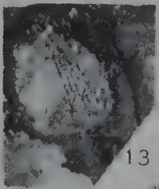
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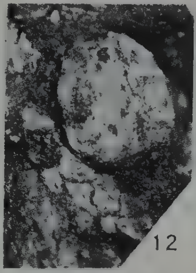
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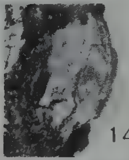
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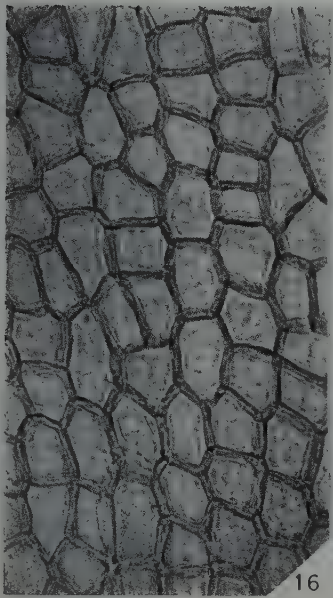
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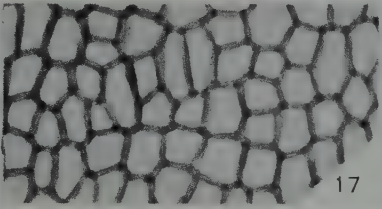
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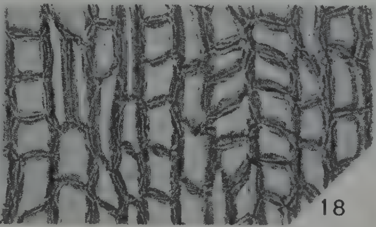
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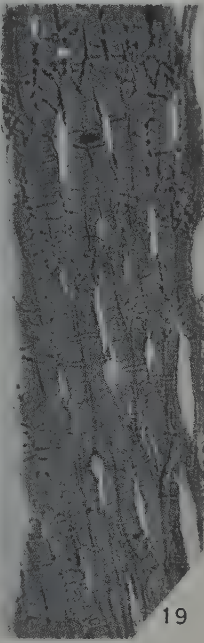
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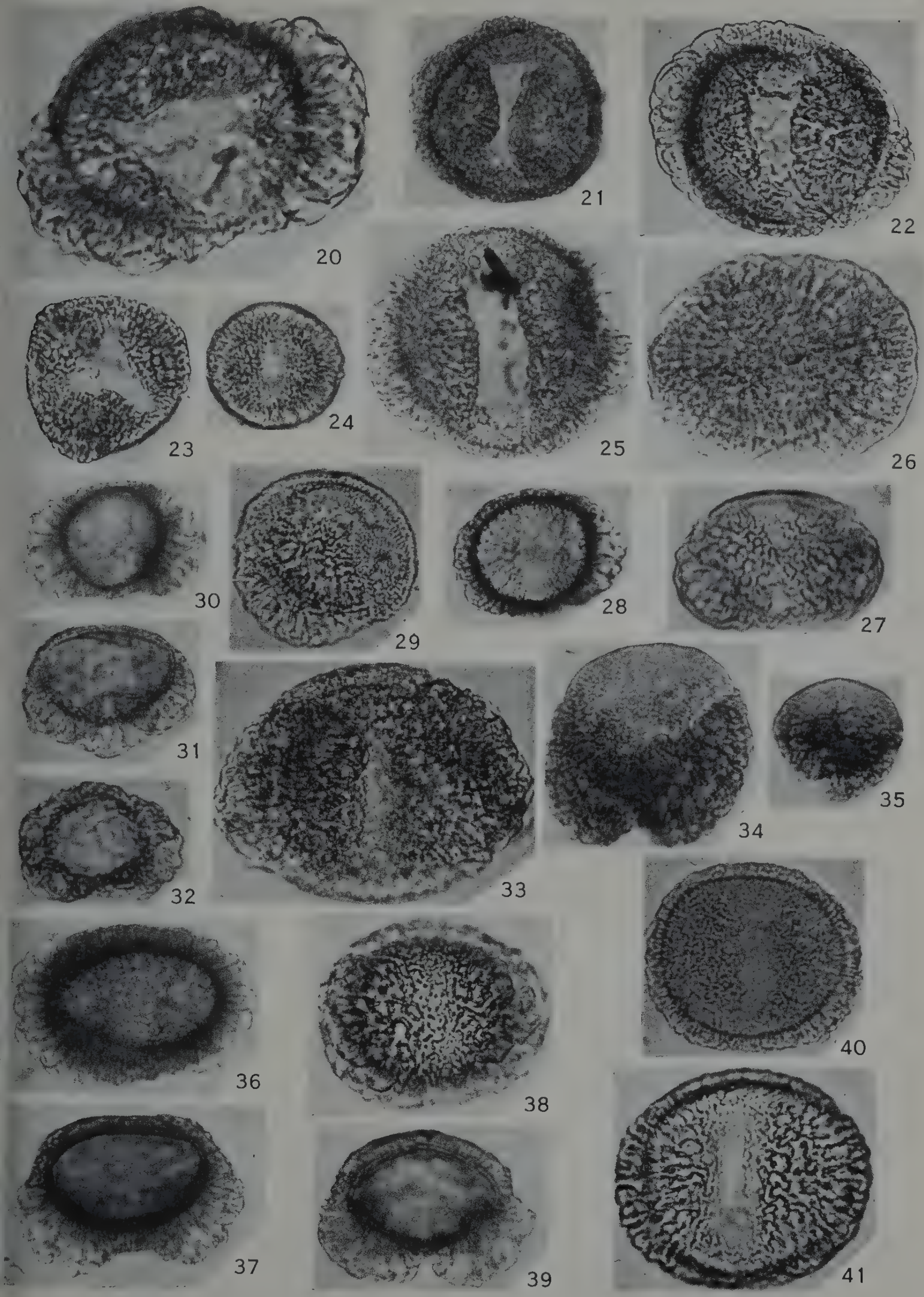
TERTIARY *DACRYDIUM* IN THE AUSTRALIAN REGION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NEW GUINEA: Shu Creek, a tributary of the Era River, south coast of Papua. Coal from a bore sunk by Australasian Petroleum Company at depths of 511, 516, 517 ft. Age: Pliocene.

Wana Well on Era River, near intersection of 144° 46½′ E. long. with 7° 24½′ S. lat. Carbonaceous clay. Age: Upper Pliocene.

Era River, north of delta area between Kikori and Purari Rivers, Papua. Coal. Age: Pliocene.

(*d*) *Comparison of the Sporomorph* Dacrydiumites florinii *with Pollen Grains of Living Species of* Dacrydium (*Group* B)

Before the sporomorph *Dacrydiumites florinii* is compared with pollen grains of individual species of *Dacrydium* (group *B*) those of two of the living species not hitherto described will be briefly considered. The descriptions and measurements which follow are based on acetolysed material.

Dacrydium araucarioides (Plate 3, Figs. 38, 39)

Grains spherical or sometimes flattened on the proximal surface, 27-44 μ in diameter, up to 59 μ in polar view when the bladders are included. Furrow indistinct. Bladders 2, rarely rudimentary, the internal thickenings forming radial loops around the margin.

Exine 2-layered, thick, about 4-5 μ, finely rugulate over the proximal surface, more coarsely and irregularly rugulate over the distal pole.

Source of material: Montagnes des Sources, New Caledonia. Buchholz 1059.

Dacrydium balansae (Plate 3, Figs. 36, 37)

Grain more or less spherical, sometimes slightly flattened on the proximal surface, length of body 31-48 μ, overall length of grain, including the bladders, up to 59 μ. Furrow not clearly defined. Bladders 2, the internal thickenings forming radially directed loops.

Exine 2-layered, about 4-5 μ thick, finely rugulate over the proximal surface, more coarsely so over the distal pole.

Source of material: Virot No. 187. Mt. Dzumac, New Caledonia; per late Professor J. T. Buchholz.

The size range (23-78 μ) and diversity of form of the sporomorph *Dacrydiumites florinii* are considerably greater than that of the pollen grains of any of the living species examined. A somewhat comparable size range has been observed in pollen of *Dacrydium elatum* (31-60 μ) but in that of *D. araucarioides, D. balansae,* and *D. cupressinum* the range does not exceed 17 μ. Again the degree of development of the bladders is far more variable in *Dacrydiumites florinii* as defined here than it is in recent species, with the possible exception of *Dacrydium cupressinum* in which, as Cranwell (1941) points out, the bladders are "normally two, small, often rudimentary, forming a scalloped frill around the furrow or an inconspicuous irregular cover traceable because of its coarse reticulation. Three bladders may merely be suggested, the furrow area then being roughly triangular."

In many of the grains of *Dacrydiumites florinii* the exine in the furrow region is coarsely sculptured as it is in *D. balansae, D. araucarioides,* and apparently in some grains of *D. cupressinum.* In others, as also in the pollen of *D. elatum,* the furrow is well defined and the furrow membrane smooth.

The exine of the cap seems to be rather thinner and more delicate than in pollen grains of the living species examined.

On the whole it may be said that a higher maximum body diameter and more prominent bladders have been observed amongst the pollen grains included in the sporomorph *Dacrydiumites florinii* than in the pollen of recent species of *Dacrydium* (group *B*).

(*e*) *Geological Range of* Dacrydiumites florinii

Many of the deposits in which *D. florinii* occurs are not closely associated with marine strata containing reliable zone fossils, so that their age has not been precisely determined. However, if the recent opinions put forward by Raggatt and Crespin (1952, Fig. 1, p. 146) and Gill (1952) are correct, the geological range of *D. florinii* in Victoria is from Palaeocene (Eastern View) to Upper Pliocene (Hamilton). This would mean that the withdrawal of *Dacrydium* (group *B*) from this region must have taken place after the Upper Pliocene.

The present investigation has also shown that a species of *Dacrydium* (group *B*) was in existence in New Guinea during Pliocene times. No information regarding its early Tertiary history has as yet been obtained. It is of interest that Couper (1952) recorded a pollen type, *Dacrydium praecupressinoides*, presumably related to *Dacrydiumites florinii*, from the Early Tertiary of New Zealand, and pollen of *Dacrydium cupressinum* from Pliocene and younger deposits (Couper 1951).

IV. ACKNOWLEDGMENTS

Specimens of living species of *Dacrydium* were kindly supplied by Dr. G. Taylor, British Museum (Natural History); the late Professor J. T. Buchholz; Professor C. G. G. J. van Steenis, Leiden, Holland; Professor H. Holttum, University of Malaya; Mr. R. H. Anderson, Botanic Gardens, Sydney; Mr. A. W. Jessep, National Herbarium of Victoria; Mr. W. F. Harris, D.S.I.R., New Zealand; and Mr. J. S. Womersley, Lae, New Guinea.

Geological samples from Tasmania and New Guinea were generously provided by Professor S. Warren Carey, University of Tasmania, and Mr. J. N. Montgomery, Australasian Petroleum Company, Melbourne, respectively.

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Explanation of Plates 1-3

All the figures are from untouched negatives

Plate 1

Dacrydium rhomboideum sp. nov.

Fig. 1.—Portions of sterile foliage shoots. Natural size. Nat. Mus. Vic. No. P. 15583.

Fig. 2.—A branched shoot. × 5. Nat. Mus. Vic. No. P. 15584.

Fig. 3.—A shoot with a lateral bud. × 5. Nat. Mus. Vic. No. P. 15585.

Fig. 4.—Transverse section of a shoot. × 60. Nat. Mus. Vic. No. P. 15586.

Fig. 5.—Cuticle of apical region of leaf showing ctenoidally arranged marginal cells. × 150. Nat. Mus. Vic. No. P. 15587.

Fig. 6.—Cuticle of an entire leaf. × 150. Nat. Mus. Vic. No. P. 15588.

Fig. 7.—Cuticle of leaf opened out to show the arrangement of the stomata on the upper and lower surfaces. × 120. Nat. Mus. Vic. No. P. 15589.

Fig. 8.—Portion of transverse section of leaf showing thick-walled epidermal cells and two stomata, the guard cells of which are overarched by outgrowths from the subsidiary cells. × 600. Nat. Mus. Vic. No. P. 15590.

Fig. 9.—Epidermis and hypodermis of leaf in transverse section. × 600. Nat. Mus. Vic. No. P. 15591.

Plate 2

Fig. 10.—*Dacrydium rhomboideum.* Two stomatal groups from the upper epidermis of a leaf. × 600. Nat. Mus. Vic. No. P. 15592.

Fig. 11.—*Dacrydium rhomboideum.* Cells of the lower epidermis with thick, pitted, undulate lateral walls. × 600. Nat. Mus. Vic. No. P. 15724.

Figs. 12-14.—*Dacrydium rhomboideum.* Seeds. × 5. Nat. Mus. Vic. Nos. P. 15725, 15726, 15727 respectively.

Fig. 15.—*Dacrydium cupressinum.* A seed. × 5.

Fig. 16.—*Dacrydium rhomboideum.* Cuticle of integument of seed. × 200. Nat. Mus. Vic. No. P. 15728.

Fig. 17.—*Dacrydium araucarioides.* Cuticle of integument. × 200.

Fig. 18.—*Dacrydium cupressinum.* Cuticle of integument. × 200.

Fig. 19.—*Dacrydium rhomboideum.* Section through stony layer of the integument. × 200. Nat. Mus. Vic. No. P. 15729.

Plate 3

The pollen grains are magnified 600 diameters. Figures 20-35 illustrate the sporomorph *Dacrydiumites florinii* from various localities in Australia and New Guinea.

Figs. 20, 21.—Vegetable Creek, N.S.W.

Figs. 22-24.—Brown coal, Yallourn, Vic.

Fig. 25.—Lal Lal, Vic. Mines Dept. Bore 47 at 216-223 ft.

Fig. 26.—Eastern View, Vic.

Fig. 27.—Hamilton, Vic.

Fig. 28.—Wensleydale, Vic.

Fig. 29.—Brown coal, Moorlands, S.A.

Fig. 30.—Cootabarlow, S.A.

Figs. 31, 32.—Near Denmark, W.A.

Figs. 33-35.—Shu Creek, Papua, New Guinea. Aust. Pet. Co. Bore at 511 ft.

Figs. 36, 37.—*Dacrydium balansae.* Virot. No. 187. Mt. Dzumac, New Caledonia, per late Professor J. T. Buchholz.

Figs. 38, 39.—*Dacrydium araucarioides.* Montagne des Sources, New Caledonia. Buchholz. 1059.

Fig. 40.—*Dacrydium cupressinum.* Dominion Museum, Wellington, N.Z., per W. F. Harris.

Fig. 41.—*Dacrydium elatum.* Penang Hill, 2500 ft. Malaya, per Professor R. Holttum.

THE VEGETATION OF THE SOUTH-EASTERN RIVERINA, NEW SOUTH WALES

I. THE CLIMAX COMMUNITIES

By C. W. E. Moore *

[*Manuscript received October* 20, 1952]

Summary

The results of an ecological survey of the south-eastern Riverina are presented. The general features of the environment (climate, geology, physiography, and soils) are described.

Twenty-three plant associations are recognized and described and these are grouped into seven alliances and two formations. The distribution of the alliances is shown on the vegetation map of the region.

The relationships between the vegetation and environmental factors are discussed. There is little correlation between the vegetation and geological formations. The distribution of the communities does not appear to be closely related to climatic factors, chiefly owing to the over-riding effects of soil and topography.

Evidence is presented to show that the grasslands in the Narrandera, Urana, Jerilderie area are disclimax communities developed from the *Acacia pendula-Atriplex nummularia* Alliance.

The life-form spectra of each alliance and of the whole region are given and briefly discussed. There is a preponderance of hemicryptophytes and therophytes except in the *Eucalyptus dealbata-E. sideroxylon* Alliance which is strongly nanophanerophytic.

The appendix gives a species list for each alliance, together with notes on the occurrence of species rarely found in the region.

I. INTRODUCTION

Though the need for an ecological survey of New South Wales has long been recognized, broad-scale mapping and classification of the vegetation communities has not been attempted until recent years. Maiden (1897, 1901) and Cambage (1925) both realized the advantages that would result from a botanical survey of New South Wales, but little was accomplished until Pryor (1939) described and mapped the vegetation of the Australian Capital Territory. This was followed by the work of Pidgeon (1942) in the central coastal area. The greatest contribution to date has been made by Beadle (1948) who described and mapped the communities of the Western Division. Morland (1949, 1951) has described the communities in the New South Wales portion of the Murray River catchment, and Costin (1952) has described and mapped the vegetation of the Monaro region. The work reported here is a further contribution to the study of the vegetation of the State as a whole, and to the eventual production of a vegetation map of New South Wales.

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* Division of Plant Industry, C.S.I.R.O., Canberra, A.C.T.

(*a*) *Objectives and Methods*

The primary objectives have been the mapping, description, and classification of the major climax communities, and the determination, as far as practicable on a broad scale, of the relationships between these communities and their environment. A climax community is a community in equilibrium with its environment, i.e. it is essentially a stable community over a relatively long period. In the present work the term is restricted to stable communities which existed prior to the advent of the white settler. When a community undergoes changes of a greater or lesser degree as a direct result of the activities of man (such as clearing, grazing, burning, etc.) the resultant community is a disclimax. It is believed that a proper basis for the study of a disclimax community is a knowledge of the composition, structure, and distribution of the climax from which it has been derived. Hence an attempt has been made to determine, as far as possible, the composition and structure of the communities present prior to white settlement.

This becomes more and more difficult with the passage of time. Many changes in the flora and in the composition and structure of the plant communities have been induced as a result of settlement of the region, which proceeded rapidly between 1829 and 1845 following the favourable reports of the early explorers (see Gormly 1906; Bayliss 1914; Andrews 1920). After the passing of the Robertson Land Act in 1862 there was a large influx of free selectors, and during the last 50 years there has been an increasing tendency to subdivision of the land into smaller holdings with further destruction of the native flora.

Unfortunately there are few, if any, relict areas in which the original conditions have been preserved. Even in communities which do not provide useful timber, and in which there is not a sufficient depth of soil to warrant clearing for grazing or cultivation, the original shrub and herbaceous strata have been modified by fire and rabbits.

The brief notes on the vegetation by the early explorers indicate that the woodlands were open communities with a well-developed herbaceous stratum in which the dominant species was almost certainly *Themeda australis.* (Sturt 1834; Hovell and Hume 1837; Andrews 1920). Sturt makes frequent reference to "honeysuckle scrub" (*Banksia marginata*), which he noted as far west as Narrandera. This species does not now occur west of the Tablelands, though some of the older residents of the Narrandera district can clearly recollect it. It is now impossible to determine how many species have similarly disappeared.

Besides the loss of native species, changes have been brought about by the introduction of a large number of exotics which have affected the communities directly by their presence and indirectly through competition with the endemic species.

The method employed was essentially one of road survey. Practically all negotiable roads and tracks were traversed, notes being made on the general features of the vegetation, soils, geology, and topography, distances being recorded from speedometer readings. Frequent stops were made for detailed examination of vegetation and soils, and the collection of botanical specimens.

and soil samples. Specimens of practically all the plants recorded have been preserved in a special collection at the Division of Plant Industry, Canberra, A.C.T. A few of the rare species have been preserved in the Plant Industry Herbarium. Areas inaccessible by motor vehicle were inspected on foot.

The mapping of the community boundaries has been greatly facilitated by the use of aerial photographs. Without these the accuracy of the mapping would have been very much reduced, and only approximate boundaries of many of the communities could have been drawn.

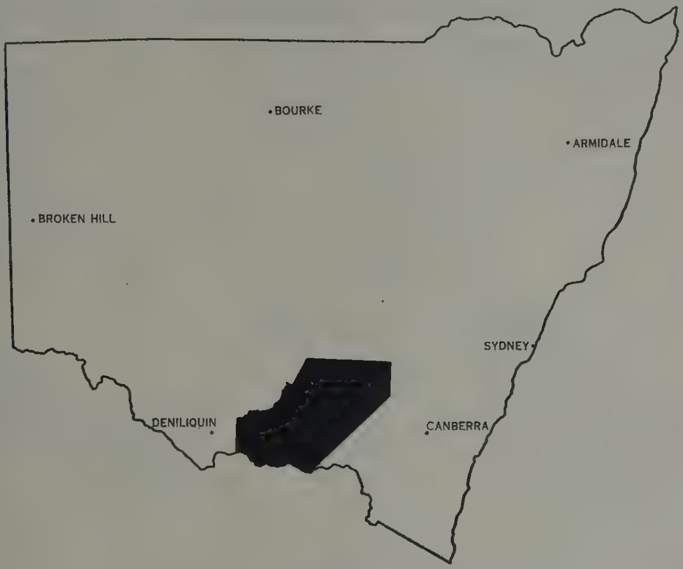


Fig. 1.—Location of the south-eastern Riverina in New South Wales.

(*b*) *Definition of the Region*

The region surveyed is a portion of the south-west slopes and adjacent plains, covering some 13,000 sq. miles. The western boundary corresponds to the southern part of the eastern boundary of the area mapped by Beadle (1948), approximately from Ardlethan through Narrandera to Tocumwal. On the south the area is bounded by the Murray River from Tocumwal to Albury. The eastern boundary passes through Albury and Gundagai, thence northwards to a point between Young and Boorowa, and the northern boundary is approximately an east-west line passing through a point a little to the north of Young. The area in relation to the whole of New South Wales is shown in Figure 1.

II. The General Features of the Environment

(*a*) *Climate*

The region comprises a portion of the Murray River basin as defined by Fenner (1934), the climate of which he describes as "that of an interior lowland in the cool temperate zone." The greater part of the rain falls in the winter, though summer thunderstorms are common. The winters are mild, with few frosts, while the summers are hot and dry. The annual evaporation greatly exceeds the annual precipitation.

(i) *Rainfall.*—Rainfall data have been obtained from records published by the Commonwealth Bureau of Meteorology (Anon. 1948). Figure 2 shows the 16, 19, 22, and 25 in. isohyets for the area. One of the most important rainfall characteristics, viz. the rapid decrease in total precipitation from east to west, is clearly seen. The mean annual precipitation at Albury is 27.50 in., while at Tocumwal it is only 16.56 in., a decrease of 11 in. in a distance of only about 75 miles. The lowest annual rainfall occurs at Jerilderie (15.05 in.).

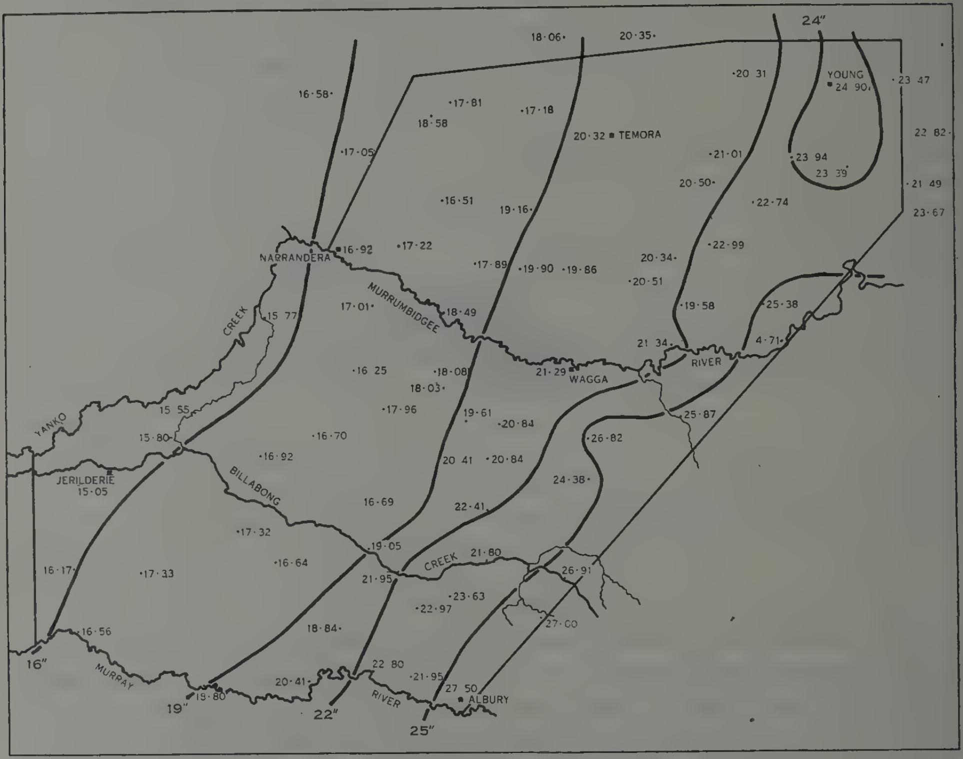

24″
18·06
20·35
20 31
YOUNG
24 90
23 47
16·58
17·81
17·18
18·58
20·32
TEMORA
22 82
17·05
21·01
23 94
23 39
20·50
21 49
16·51
19·16
22·74
23·67
NARRANDERA
16·92
17·22
22·99
17·89
19·90
19·86
20·34
20·51
MURRUMBIDGEE
CREEK
15 77
17·01
18·49
19·58
25·38
21 34
4·71
RIVER
16 25
18·08
18·03
21·29
WAGGA
YANKO
15 55
17·96
19·61
20·84
25·87
15·80
16·70
26·82
16·92
20 41
20·84
JERILDERIE
15·05
BILLABONG
24·38
16·69
22·41
17·32
19·05
16·17
17·33
16·64
CREEK
21·80
21·95
26·91
23·63
22·97
16·56
18·84
27·00
16″
MURRAY
22 80
21·95
20·41
27 50
ALBURY
19·80
19″
RIVER
22″
25″

Fig. 2.—Mean annual rainfall of the south-eastern Riverina.

Figure 3 shows the median monthly rainfall and the upper and lower quartiles for six stations. The greater proportion of the rain falls in the winter months (June, July, and August) over the whole area, though there is a tendency to a flattening of the median curve in the more westerly stations (Urana, Narrandera, and Berrigan). Though median monthly values during the summer are commonly more than 1 in., the effectiveness of the rain during this period is normally slight owing to high temperatures and rapid evaporation. The effectiveness of summer rain is further reduced by excessive run-off since precipitation during this period is commonly in the form of thunderstorms with downpours lasting only a short time.

The variability of the rainfall is indicated in Figure 3 by the upper and lower quartiles of the monthly precipitation. It is seen that there is considerable variability in the rainfall for any month from year to year, and that this variability is similar for all stations.

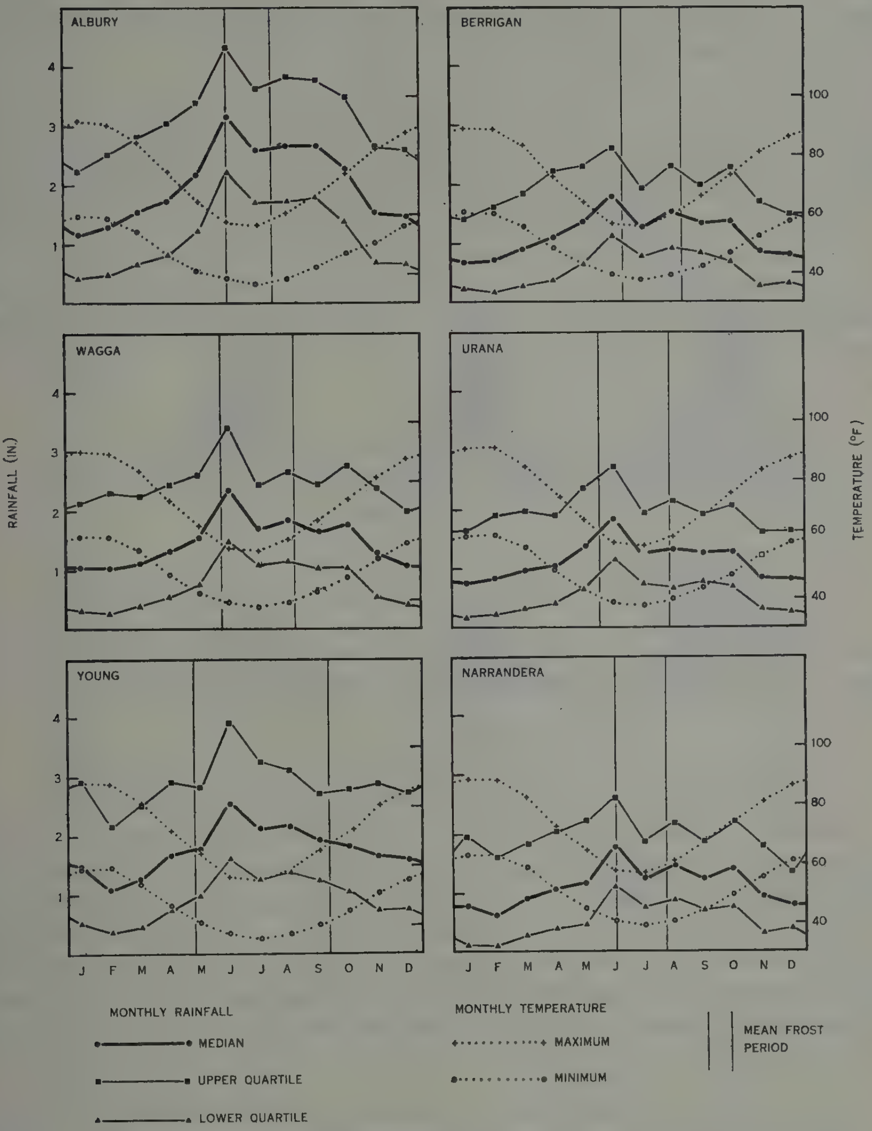


Fig. 3.—Monthly rainfall (median, upper and lower quartiles), mean maximum and minimum temperatures, and mean frost period for six stations. (No temperature and frost data are available from Narrandera, and the figures for Leeton have been used.)

Though summer rainfall commonly occurs as scattered thunderstorms of greater or less severity, tropical depressions sometimes move far enough to the south to cause general rain throughout the area. The higher summer rainfall to the north, as indicated by the records for Young, is due to the more frequent influence of these tropical depressions in this part of the region than towards the southern boundary.

(ii) *Temperature and Occurrence of Frosts.*—Mean monthly maximum and minimum temperatures are shown for six stations in Figure 3. There is a remarkable uniformity in temperature throughout the area. As temperatures fall during the winter, rainfall increases, while during the summer period of minimum rainfall, temperatures reach a maximum.

The mean monthly temperature range is fairly high, the greatest range occurring during the summer (15.9-17.4F° in December) and the smallest during the winter (9.6-11.4F° in June). The lowest mean monthly temperature occurs in July, and the highest in January. The mean annual range varies from 28.5 to 30.6F°.

TABLE 1

MEAN MONTHLY RELATIVE HUMIDITY AT THREE STATIONS

Stations	Relative Humidity (%)											
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Albury	47	52	58	68	81	87	87	81	69	60	52	47
Wagga	49	53	59	69	80	89	88	82	73	63	50	48
Cootamundra	61	66	70	78	86	90	91	85	77	69	63	60

The mean date on which the first and last screen temperatures of 32°F occur are shown in Figure 3 for six stations (Foley 1945). The frost period is short throughout the area, except towards the north-east (Young) where frosts may be expected over a period of 5 months. This longer frost period in the north-east is related to the greater altitude here than throughout the region generally. Undoubtedly relatively long frost periods would be recorded for the higher country near the eastern boundary were there any suitably placed recording stations.

(iii) *Humidity.*—Records of relative humidity are available for only three stations, viz. Albury, Wagga, and Cootamundra. The figures were supplied by the Commonwealth Bureau of Meteorology and are the mean monthly values at 9.00 a.m. (Table 1). The most notable feature is the low summer and high winter values.

(iv) *Precipitation/Evaporation Ratios.*—Prescott (1951) and Prescott and Thomas (1949) have shown that the value of $P/E^{0.75}$ gives a more satisfactory index of rainfall efficiency than the Meyer ratio (P/s.d.) or the Transeau ratio (P/E), and have also pointed out that limiting values must be chosen to fit the special requirements of the moment. Since records of evaporation are rarely kept, figures for evaporation have been calculated from the formula

$$E = 21.2 \text{ s.d. (Prescott 1938)}$$

for all stations except Young, for which evaporation data have been published by the Commonwealth Bureau of Meteorology (Anon. 1948). (Since humidity records are not available for Young, it was not possible to use the formula $P/\text{s.d.}^{0.75}$ throughout.) Mean monthly values for $P/E^{0.75}$ for six stations are shown in the form of histograms in Figure 4. It is clear from the figure that moisture conditions are limiting for growth during the summer period, while adequate moisture supplies are available during the winter.

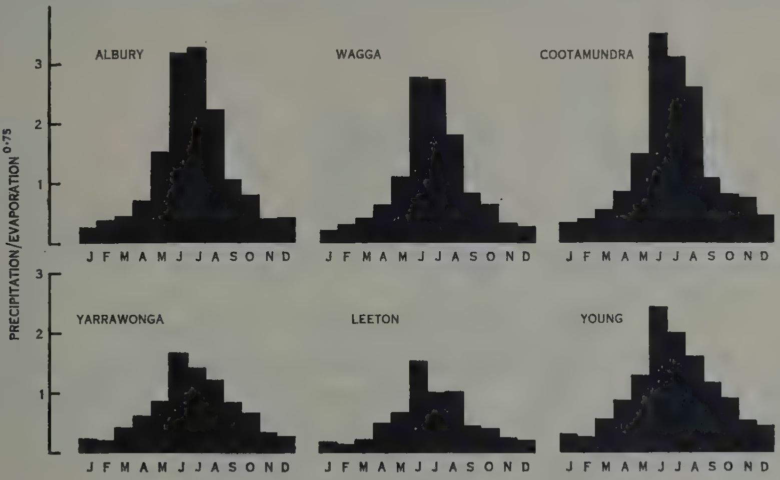


Fig. 4.—Mean monthly Precipitation/Evaporation$^{0.75}$ for six stations. (Yarrawonga is a Victorian station on the southern side of the Murray River opposite Mulwala. The figures for Leeton are used as this is the nearest station to Narrandera.)

Table 2 gives the monthly values of the climatic index of rainfall efficiency ($P/E^{0.75}$) for different levels of soil moisture and vegetation needs as suggested by Prescott and Thomas (1949).

TABLE 2

MONTHLY VALUES OF THE CLIMATIC INDEX OF RAINFALL EFFICIENCY $P/E^{0.75}$ FOR DIFFERENT LEVELS OF SOIL MOISTURE AND VEGETATION NEEDS (PRESCOTT AND THOMAS 1949)

For the break of the season	0·4
For vegetation of low transpiration or for start of drainage through bare soil	0·8
For vegetation of average transpiration and catchment areas	1·2
For high transpiration	1·6
For rice fields	2·0

The number of consecutive months during which the monthly values of $P/E^{0.75}$ are equal to or exceed the limits shown in Table 1 are given for the six stations in Table 3.

(v) *Evaporation.*—Evaporation data are available only for Young, and for other stations have been calculated from the formula

$$E = 21.2 \text{ s.d. (Prescott 1938).}$$

Mean annual evaporation and mean annual precipitation for six stations are given in Table 4. It is clear from the data that mean annual evaporation greatly exceeds mean annual precipitation.

TABLE 3

NUMBER OF CONSECUTIVE MONTHS DURING WHICH THE MONTHLY VALUES OF $P/E^{0\cdot75}$ ARE EQUAL TO OR EXCEED THE LIMITING VALUES GIVEN BY PRESCOTT AND THOMAS (1949)

Station	<0·4	>0·4	>0·8	>1·2	>1·6	>2·0
Albury	2	10	6	4	3	3
Yarrawonga* ..	4	8	5	3	1	—
Wagga	4	8	5	3	3	2
Leeton** ..	5	7	3	1	—	—
Cootamundra ..	1	11	7	4	3	3
Young	1	11	7	4	3	3

*A Victorian Station on the southern side of the Murray River opposite Mulwala.
**Nineteen miles north-west of Narrandera.

(*b*) *Geology, Physiography, and River Systems*

(i) *Geology.*—The following account of the geological formations has been extracted from David (1950). The geological map (Fig. 5) has been slightly modified from the regional geological maps published by the Division of Reconstruction and Development, Premier's Department, Sydney.

TABLE 4

MEAN ANNUAL EVAPORATION AND MEAN ANNUAL PRECIPITATION FOR SIX STATIONS

Station	Mean Annual Evaporation (in.)	Mean Annual Precipitation (in.)
Albury	57·24	27·50
Yarrawonga*	53·85	19·51
Wagga	56·39	21·29
Leeton†	67·84	15·88
Cootamundra	38·58	22·74
Young	44·27	24·90

*A Victorian Station on the southern side of the Murray River opposite Mulwala.
†Nineteen miles north-west of Narrandera.

The south-west slopes consist chiefly of Upper Ordovician and Silurian sediments interrupted by granites belonging to at least three epochs of intrusion. The rocks are for the most part blue-black carbonaceous shales and slates, with quartzites, cherts, and rarely a little limestone, but in places coarser sediments may appear with tuff-beds. They have all been subjected to folding, usually of much intensity, and there are areas in which they have suffered considerable regional and local metamorphism.

At Albury the meta-sediments consist mainly of two-mica schists, coarse and fine, some of which contain porphyroblasts of andalusite; sillimanite is also present, and there is local granitization. Somewhat similar rocks are to be found round Wagga Wagga, whence phyllites, knotted schists, cordierite-bearing mica-schists, and quartz-granulites have been reported. Schists and phyllites locally grading into black slates are also known from Junee Reefs and Gundagai. Where the Ordovician Sediments have been invaded by later granites, they have proved very susceptible to local metamorphism, with the formation of hornfels and less completely altered types.

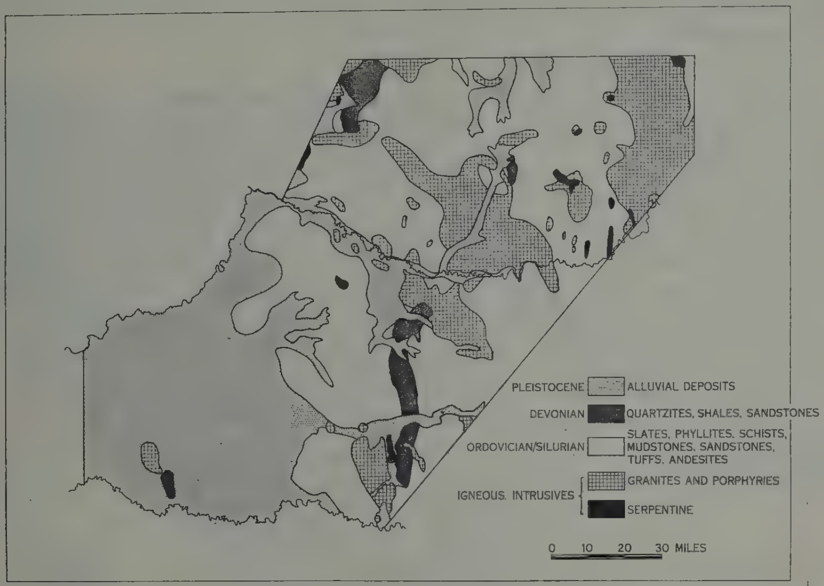

PLEISTOCENE
ALLUVIAL DEPOSITS
DEVONIAN
QUARTZITES, SHALES, SANDSTONES
ORDOVICIAN/SILURIAN
SLATES, PHYLLITES, SCHISTS, MUDSTONES, SANDSTONES, TUFFS, ANDESITES
IGNEOUS INTRUSIVES
GRANITES AND PORPHYRIES
SERPENTINE
0 10 20 30 MILES

Fig. 5.—Geological map of the south-eastern Riverina. (Slightly modified from the regional maps prepared by the Premier's Department, Sydney.)

Within the area there are a few relatively small outcrops of Devonian sediments. The more important of these occur near Narrandera and Ardlethan, between Wagga and Henty, and in the Yambla Range north of Albury. They are composed of purplish or reddish sandstones, white quartzites and conglomerates, and pebbly grits, with beds of vividly red sandstone or shale.

A few miles to the west of Wallendbeen there is a small area of basalt (not shown on the map and not mentioned in David's account of the geology of the region). From its similarity to the basalts of other regions (e.g. Crookwell and Dubbo) it appears likely that this is Tertiary basalt.

The Western Plains consist of mixed alluvial deposits of Pleistocene and Recent origin.

(ii) *Physiography.*—The physiography of the region is shown in Figure 6. The highest peak reaches only 2,430 ft above mean sea-level. The greater part of the region (91 per cent.) is below 1,500 ft, while 67 per cent. is under 1,000 ft, and 31 per cent. below 500 ft above sea-level. Most of the country is undulating to hilly, especially in the northern half and the south-eastern quarter. In the south-west the topography is flat or undulating. A relatively small area of steep and rugged country occurs, chiefly towards the eastern boundary, but also in the Ardlethan district. The most extensive areas are the Yambla Range extending southwards from Culcairn, the ranges to the west and south of Cootamundra, and some of the relatively high land near the eastern boundary from the Murrumbidgee River southwards to Holbrook. It is of interest to note that the steeper slopes frequently occur on the western aspects of the ranges, the eastern slopes being much more gentle. This is particularly well shown on the Yambla Range and on the ranges to the south of Cootamundra.

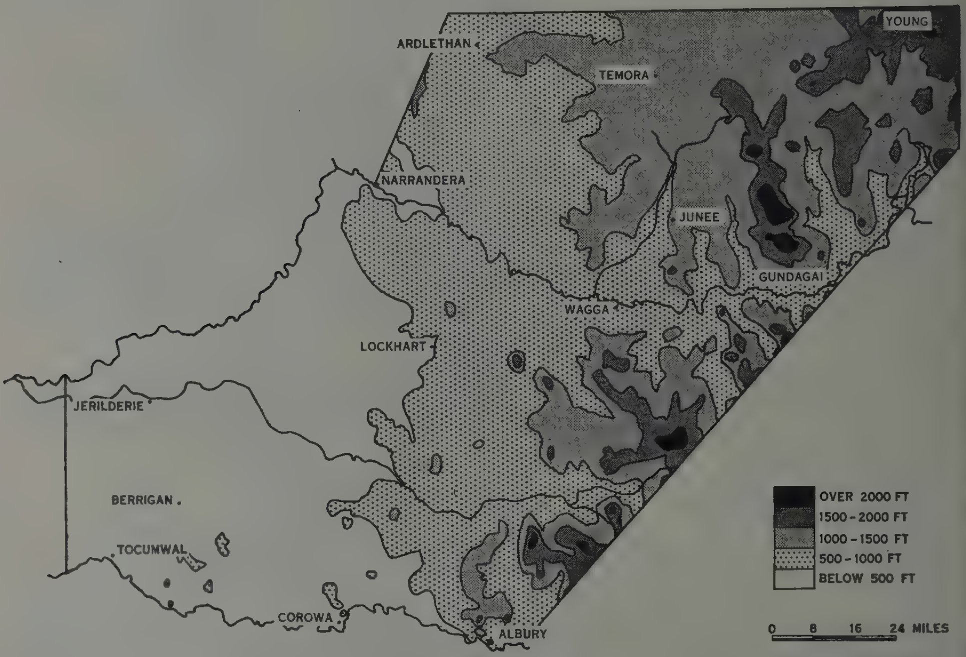


Fig. 6.—Physiographic map of the south-eastern Riverina. (From contours supplied by the Geology School, University of Melbourne.)

(iii) *River Systems.*—Since the region is bounded on the east by the slopes of the Dividing Range, and there is a general fall towards the west, practically the whole of the drainage is in that direction. The low ranges south of Temora constitute a portion of the divide between the Murrumbidgee and Lachlan catchments so that the drainage from a small area is northwards to the latter river. All water drained from the area eventually reaches the Murray River. There are three main streams, the Murray River, the Murrumbidgee River, and Billabong Creek. Two subsidiary creeks leave the Murrumbidgee near Narrandera and meander across the plains in a south-westerly direction, eventually emptying into Billabong Creek. The main streams are shown in Figure 6, and also in the vegetation map.

Butler (1950) presents a new theory of "prior streams" for the region, part of which is within his "Riverine Plain." According to this theory, the present river system is not an old one as has been suggested by previous writers (Gregory 1904; Hills 1940; Browne 1945), but the alluvial deposits on which the present soils have been formed were brought down by "prior streams," and the present streams are, in fact, eroding new channels through these deposits, not depositing sediments. The formation and structure of the soil have been determined in large measure by deposits from, and flooding by, the old streams, modified by climate, topography, and flooding by the present streams where this occurs.

(*c*) *Soils*

There is little published information about the soils of this part of New South Wales. Jensen (1914) described and classified the soils of New South Wales on a geological basis, but as Prescott (1931) has pointed out, his system was not suitable for a complete account of the soils. Prescott (1931, 1944) has given a general description and map of the major soil groups of Australia, and in his earlier publication he indicated the general relationships between soils and vegetation. It cannot be expected that a map of the scale produced by Prescott (1944) can do more than show the general distribution of the major soil groups, and to this extent its application to a relatively small area is limited.

Little detailed work has as yet been done in this region. Smith (1945) made a soil survey of the Berriquin Irrigation District, which includes a small portion to the south-west. A detailed survey of a neighbouring area, including many of the same or similar soil types, has been made by Butler *et al.* (1942).

Six soil groups as suggested by Stephens (1950*a*) have been recognized within the region, viz.:

(1) Undifferentiated skeletal soils;

(2) Red podsolic soils;

(3) Yellow podsolic soils;

(4) Red-brown earths;

(5) Grey soils of heavy texture;

(6) Brown soils of heavy texture.

The relationships between these and similar soils in North America and Europe have been discussed by Stephens (1950*b*).

A further group of chocolate soils, as proposed by Hallsworth *et al.* (1952) occurs on a limited area of basalt a few miles to the west of Wallendbeen.

For the purposes of discussion in this paper the red podsolics are grouped with the yellow podsolics, and the grey soils of heavy texture are grouped with the brown soils of heavy texture. The major features of each group are given below, and approximate boundaries of the more important groups are given in Figure 7. The distribution of the skeletal soils can best be seen on the vegetation map, since it corresponds closely with the distribution of the Dry Sclerophyll Forest communities.

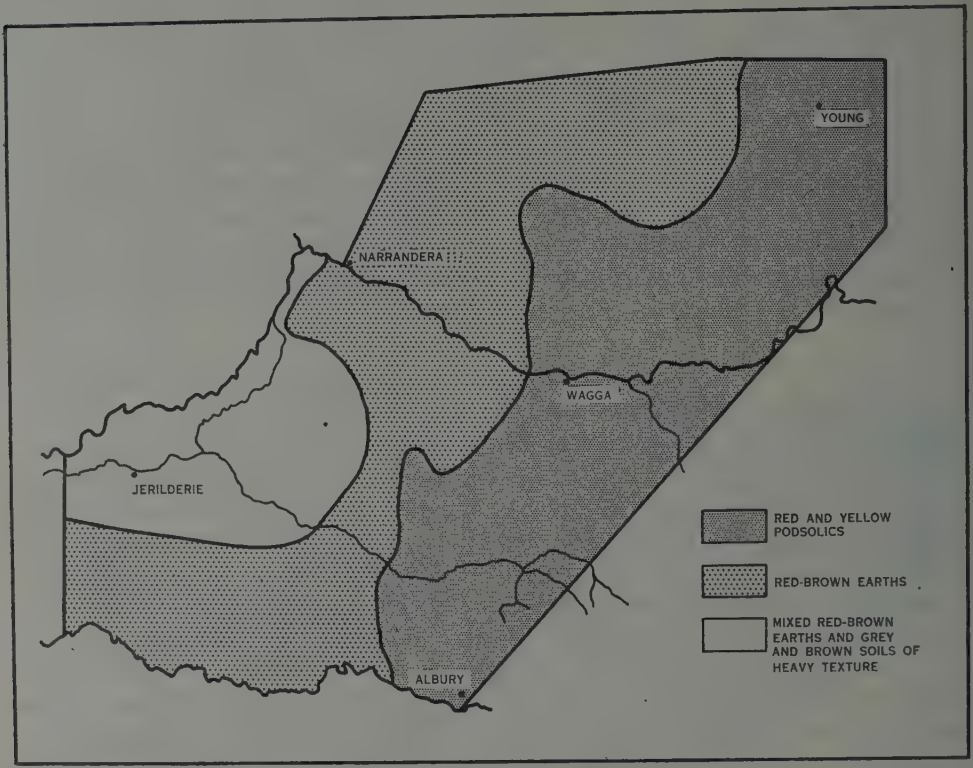


Fig. 7.—Approximate boundaries of the major soil groups of the south-eastern Riverina.

(1) The undifferentiated skeletal soils occur on the more or less rocky outcrops, and are characterized by little or no profile development. On the steeper slopes excessive erosion during heavy falls of rain prevents the accumulation of the soil (Prescott 1944; Beadle 1948), and the excessive run-off results in a condition of aridity. On the more gentle slopes accumulation of soil particles can occur, and some profile development is evident. The stage of development of the soil depends in large measure on the degree of erosion, which itself depends on the slope and vegetative cover. In the better-developed soils of this group, distinct A and B horizons can be recognized. The texture of the soils varies according to the nature of the parent material and the degree of leaching that has occurred.

(2) The red and yellow podsolic soils are not true podsols. In this region leaching has not been sufficient to mobilize the iron in the surface, though clay has accumulated in the illuvial horizon. Prescott (1944) states that these soils are a transitional form developed in the less humid regions, largely on sandy parent materials.

The topography where the red and yellow podsolics occur is typically rolling to hilly, and leaching has proceeded to a greater degree at low levels where moisture supply is greatest than on the slopes and tops of the hills.

(3) The red-brown earths have been described by Prescott (1944). In these soils there is an accumulation of clay and usually of free calcium carbonate in the illuvial horizons. Calcium carbonate may be lacking if the parent materials are deficient in lime. The leaching is not sufficiently active to mobilize the iron oxide independently of the clay. The texture of the A horizon is most commonly sandy loam or loam, though it may range from sands to clays. These soils occur in zones of seasonal rainfall, and Prescott (1944) suggests that "the relative stability of the iron oxides is due in part to the effect of the annual drying out of the soil associated with the season of drought."

The red-brown earths cover a large proportion of the region, and are developed on the Recent and Pleistocene alluvial deposits of the plains, on granite, and on the Ordovician and Silurian sediments. They are found chiefly to the west of the 22-in. isohyet, and are of considerable economic importance in that they constitute the chief wheat-growing areas of southern New South Wales.

(4) The grey and brown soils of heavy texture are characterized by the presence of calcium carbonate, which may be present from the surface horizon down. Gypsum is frequently present in the deeper illuvial horizons. The surface soil generally has a nutty or crumb structure, while the subsoil is cloddy. They are usually uniformly grey or brown throughout the profile. The texture varies from clay loam to heavy clay. Prescott (1944) considers that these soils are members of Marbut's great group of pedocals, and that they are related to the Russian group of sierozems. The grey and brown soils of heavy texture occupy a relatively small area of the alluvial plains in the lower-rainfall areas, principally to the west of Urana, though a small area occurs on the Bullenbung Plain between Wagga and Lockhart. They frequently show crabholey structure. There is an extensive area of these soils to the west of the region. They are formed when heavy soils are found under conditions too arid for the proper development of the true black earths (Prescott 1931).

(5) The chocolate soils are developed on basaltic parent materials and are intermediate between red loams and chernozems. They are slightly acid at the surface, the pH rising in the subsoil, but there is no zone of calcium carbonate accumulation. There is little or no differentiation into horizons in the profile.

The chocolate soils near Wallendbeen fall within the reddish chocolate soils of Hallsworth *et al.* (1952) and are more closely related to the red loams than to the chernozems. Stephens (1950*b*) has included this group in the red loams.

III. The Vegetation

(*a*) *Concepts and Nomenclature in the Classification of Vegetation Communities*

In the classification of vegetation, two fundamental principles are often overlooked. The first is that it is the vegetation *per se* which is to be classified, and no factor of the habitat should be included. Relationships of the communities with their environment may or may not be demonstrated subsequently. If so, the classification will have greater practical application, but the demonstration of such relationships is not an *a priori* requirement. The second principle is that the system of classification should be consistent and applicable to the whole of the vegetation.

The work of Autralian ecologists is still handicapped by a lack of uniformity in the use of ecological terms. The confusion arises from a number of causes, amongst which are the acceptance by different ecologists of the concepts of the American, British, or European schools, the isolation of the various workers in different parts of the country, and the colouring of their views by the particular kind of vegetation with which they have to deal, and last, but by no means least, the attempt to apply the monoclimax theory (Clements 1916) to the vegetation of Australia. This results in the classification of numerous stable communities as seral, followed by attempts to explain how these communities could eventually develop into the "climatic climax." Though not belittling the value of the concept of succession and the dynamic nature of vegetation, the author is of the opinion that except in some specialized local communities or where methods such as pollen analysis may be applied, primary succession can only be satisfactory demonstrated by long-term (possibly more than the normal span of human life) and detailed studies. Theories as to long-term changes can be of little or no value if they are based on current climatic and soil conditions as it is well known that major climatic cycles, involving changes in both soil and vegetation, have occurred in the past and will no doubt occur again in the future.

Wood (1939) attempted to clarify the position by reviewing "ecological concepts from the standpoint of certain fundamental considerations and from actual experience with Australian communities." Unfortunately, he did not suggest a sound workable system applicable to the vegetation of Australia as a whole, and further he introduced the term "edaphic complex," which departs from the basic principles of classification as stated above. The "edaphic complex" (or any other complex) may frequently provide a convenient mapping unit where two or more communities form a mosaic in a region showing marked variation in the soil (or other environmental factor) over small areas, but it should not be employed in the primary classification of the vegetation. This concept has been used by a number of South Australian ecologists (Crocker 1944; Crocker and Wood 1947; Specht and Perry 1948), but the communities so grouped could as well have been grouped to show their floristic relations, rather than their edaphic relations.

The concept of the "vegetation type" was introduced by Pryor (1939) and subsequently used by Pidgeon (1942) and Beadle (1948). Pidgeon (1942) showed how the concept could be applied to all the *Eucalyptus* forests and woodlands in New South Wales, and also to similar communities in South Australia (Wood 1939). Beadle (1948) extended the concept to communities dominated by *Acacia* species, Chenopodiaceae, and Gramineae. Certain fundamental difficulties in the classification of communities dominated by *Eucalyptus* species were overcome by the use of this concept, and it can be satisfactorily applied to other types of vegetation. It has the disadvantage, however, that it is necessary to replace the *association* as the fundamental unit of classification by the *vegetation type.*

No one system of classification as developed overseas has proved entirely satisfactory for the classification of the Australian vegetation. It is necessary to modify such systems to suit the unique vegetation of this continent, and further, to define the various units employed (and particularly the fundamental unit) in such a way that it can be readily applied to any piece of stable vegetation in the field with as little difference of opinion amongst various ecologists as possible. It is probably impossible to obtain complete unanimity, since vegetation varies continuously and in several directions.

In an attempt to obtain greater uniformity in the classification of plant communities, Beadle and Costin (1952) have put forward a scheme based on the two most characteristic features of vegetation, viz. floristics and structure. This method of classification has been applied here to the vegetation of the south-eastern Riverina.

The basic floristic unit is the association which is defined as a community with the same dominant species over the whole of its range and in general having uniform structure. (This is not the same wording as used by Beadle and Costin, but there is no conflict between the two definitions.) The term is used in both the abstract and the concrete senses, and may refer to all stands having the same dominant species, or to any particular stand. The basic criterion by which the association is recognized is qualitative uniformity of the dominants. If quantitative uniformity, either of the dominants or of the members of any other stratum is insisted upon, the result is a completely unwieldy classification with innumerable associations.

An association is named by the dominant species of the tallest stratum alone provided that it is thus clearly identified (e.g. the *Eucalyptus albens* Association or the *E. dealbata-E. sideroxylon* Association). With some communities it is desirable to include a member of a lower stratum in the association name, e.g., the *Acacia pendula-Atriplex nummularia* (Shrub Woodland) Association.

The association as used here corresponds to the "vegetation type" as used by Pryor (1939), Pidgeon (1942), and Beadle (1948).

The alliance is a synthetic floristic unit defined as a group of floristically related associations of similar structure. It is named from the most characteristic dominant species of its component associations. The species selected for naming an alliance should be those which occur as dominants in as many of the component associations as possible but relatively infrequently as the dominants of associations comprising other alliances. For example, the following associations form a group of Dry Sclerophyll Forest communities of close floristic affinity and are grouped to form the *Eucalyptus dealbata-E. sideroxylon* Alliance:

Eucalyptus dealbata
E. dealbata-Acacia doratoxylon

E. dealbata-Callitris glauca
E. dealbata-E. macrorrhyncha
E. dealbata-E. sideroxylon
E. sideroxylon
E. sideroxylon-E. woollsiana
E. sideroxylon-E. polyanthemos

When an association shows little or no floristic affinity with other associations it must be regarded as an alliance of which it is the only component association, e.g. the *E. largiflorens* Alliance consists of one association only.

The alliance as here used corresponds to the association of Pryor (1939), Pidgeon (1942), and Beadle (1948).

For the higher classification categories, communities of similar structural form are grouped, irrespective of botanical composition. Thus the synthetic structural units, the formation and subformation, are obtained and are named according to the particular structural form or subform to which they belong, e.g. forest, woodland, grassland, etc. The structural forms and subforms recognized for the communities within the region are:

Structural Form	Subform
Sclerophyll Forest	Dry Sclerophyll Forest Swamp Sclerophyll Forest
Woodland	Tall Woodland Savannah Woodland Shrub Woodland

Table 5 shows the grouping of the associations into the higher classification categories.

Beadle and Costin (1952) define a shrub as "a woody plant less than about 8 metres in height (the upper limit of the microphanerophyte life form), frequently with many stems." This definition does not conform to the generally accepted meaning of the term shrub, and includes many plants commonly regarded as trees. Further, as Beadle and Costin admit, difficulties in the grouping of some associations into higher classification categories arise because of this definition. These difficulties do not occur if one adopts the more generally accepted meaning of the term. It is difficult to define a shrub as there is a gradation from the tree to the shrub habit, but the difficulty is not overcome by a rigid application of Raunkiaer's life forms to the definition.

A *shrub* is a woody plant, less than about 10 ft in height, usually without a major axis, and with the greater portion of the branches and foliage not confined to the upper half of the plant.

A *tree* is a woody plant more than 10 ft in height, usually having a major axis; the greater portion of the branches and foliage usually in the upper half of the plant.

Though exceptions will doubtless be found, these definitions should cover at least the majority of cases.

TABLE 5

GROUPING OF ASSOCIATIONS INTO HIGHER CLASSIFICATION CATEGORIES

Association	Alliance	Subformation	Formation
E. dealbata	*E. dealbata-E. sideroxylon*	Dry Sclerophyll Forest	Sclerophyll Forest
E. dealbata-Acacia doratoxylon			
E. dealbata-Callitris glauca			
E. dealbata-E. macrorrhyncha			
E. dealbata-E. sideroxylon			
E. sideroxylon			
E. sideroxylon-E. woollsiana			
E. sideroxylon-E. polyanthemos			
E. macrorrhyncha-E. rossii	*E. macrorrhyncha-E. rossii*		
E. macrorrhyncha-E. maculosa			
E. macrorrhyncha-E. polyanthemos			
E. macrorrhyncha-E. elaeophora			
E. rossii			
E. camaldulensis	*E. camaldulensis*	Closed Swamp Sclerophyll Forest and Savannah Woodland	Woodland
E. woollsiana	*E. woollsiana*	Tall Woodland	
E. woollsiana-Callitris glauca			
E. melliodora-C. glauca			
E. albens	*E. albens*		
E. albens-E. melliodora-E. blakelyi			
E. albens-E. macrorrhyncha			
E. albens-Callitris glauca			
E. largiflorens	*E. largiflorens*	Savannah Woodland	
Acacia pendula-Atriplex nummularia	*Acacia pendula-Atriplex nummularia*	Shrub Woodland	

The definitions of the Woodland and Forest formations and subformations given below have been modified from those of Beadle and Costin (1952) to conform with this definition of a shrub. Two other terms used in the text require definition, viz.:

Dominant.—A species which, because of its life form and frequency, conditions the habitats of the other members of the community (except for other dominants).

Dominant stratum.—The stratum which, because of its physiognomy and relative continuity, conditions the habitats of the other strata.

In the following descriptions of the plant communities, the most abundant species only are given. Lists of all species observed in detailed observations made in numerous stands are given in Appendix I. Brief notes on species of limited occurrence in the region and those with special habitat requirements are given in Appendix II.

(*b*) *Dry Sclerophyll Forest*

The Dry Sclerophyll Forest communities occur on the immature and skeletal soils throughout the region. These are generally closed communities dominated by sclerophyllous meso- or megaphanerophytes (rarely microphanerophytes) characterized by flat-topped crowns forming an interlacing canopy, and by boles the length of which is equal to or greater than the depth of the crowns. There is generally a well-developed but rarely continuous stratum of xeromorphic shrubs, and a poorly developed and discontinuous herbaceous stratum. The height of the dominants varies from about 20 to 60 ft or more, according to species and habitat, the lower forms developing on the most rocky sites and the taller on the deeper and more mature soils.

(i) *Eucalyptus dealbata-E. sideroxylon* Alliance.—This alliance is widespread in the southern half of New South Wales west of the Dividing Range. Its western limits have been mapped by Beadle (1948). It extends northwards at least as far as Dubbo, and eastwards beyond the boundaries of the present survey. To the east, however, as cooler and moister conditions develop with increasing altitude, it is replaced by the *E. macrorrhyncha-E. rossii* Alliance, and becomes more and more confined to the warmer and drier northern and western slopes of the hills. It does not extend beyond the south-western slopes on to the Southern Tablelands. This alliance is also widespread on the northern side of the Great Dividing Range in Victoria. Patton (1944) has described the Box-Ironbark Association for various localities in Victoria. This community is apparently the *E. sideroxylon-E. woollsiana* Association of the *E. dealbata-E. sideroxylon* Alliance. When a stand was examined near Chiltern, Victoria, it was found that the "Box-Ironbark" Association is confined to the deeper colluvial soils, while on rock outcrops at high levels the *E. dealbata-Acacia doratoxylon* Association occurs (Plate 3, Fig. 2).

The *E. dealbata-E. sideroxylon* Alliance is found on the poorer immature and skeletal soils of the low ranges throughout the region (Plates 1 and 2). It is not confined to any particular geological formation, being found on both granitic and sedimentary rocks, the latter including Devonian, Ordovician, and Silurian sediments of various kinds. Its occurrence within its climatic zone is determined by the soil conditions rather than by the nature of the parent material from which the soil is derived. It is found in areas with a mean annual rainfall of more than 26 in. in the east to less than 16 in. in the west. The precise eastern limits have not been determined.

The physiognomy and structure vary considerably, the height of the dominant trees being from about 20 ft on the poorer and drier soils supporting *E. dealbata* to 60 ft or more on the better and moister soils where *E. sideroxylon* is one of the dominants, while there is considerable variation in the associated shrub species. Communities with tall trees and a well-developed shrub stratum (e.g. *E. sideroxylon-E. woollsiana* Association) have a typical forest structure whereas at the other extreme, *E. dealbata*-dominant communities tend more towards a scrub than a forest. Tall shrubs (more than 6 ft high) are rare throughout the Alliance, while small shrubs (less than 6 ft high) are more or less abundant. The development of the shrub stratum appears to depend to a large extent on the soil conditions. The poorer and shallower soils often favour maximum shrub development, but it would appear that some other factor or factors are also involved. The herbaceous stratum is always poorly developed and may even be absent.

The *Eucalyptus dealbata* Association (Plate 2, Fig. 2) occurs on the poorest and least-developed soils, commonly at or near the tops of the low ranges, or on the rocky slopes of the higher ranges such as The Rock and Yambla Range. The trees reach a height of 20-30 ft, and the community may have the appearance of an open one since so much of the area is bare rock. *E. dealbata* grows in pockets of soil amongst the rocks, and frequently in cracks in the rocks.

Associated small trees include *Callitris glauca, C. calcarata, Brachychiton populneus, Casuarina stricta,* and *Exocarpus cupressiformis.* The most common shrubs include *Hibbertia linearis, Stypandra glauca, Acacia buxifolia, Brachyloma daphnoides,* and *Phyllanthus thymoides. Cheilanthes tenuifolia* (a xerophilous fern) is a widespread and probably almost constant member of the community, but extends to other associations within this alliance, and is also frequently found in woodland communities.

The herbaceous stratum is always poorly developed, and is found chiefly in small pockets of relatively deep soil, especially if it is at the same time well supplied with organic matter. Common species include *Stipa falcata, Danthonia* spp., *Crassula sieberiana, Geranium pilosum,* and *Hypochoeris radicata.*

The *Eucalyptus dealbata-Acacia doratoxylon* Association (Plate 3, Figs. 1 and 2) is found in situations similar to those of the *E. dealbata* Association, but is more common on the warmer sites towards the west of the region, or on steep northern and western slopes. In general structure, physiognomy, and associated species, it is similar to the *E. dealbata* Association.

The *Eucalyptus dealbata-Callitris glauca* Association (Plate 4, Fig. 1) develops on soils which are of a coarse sandy texture and in situations which commonly receive additional water in the form of run-off from higher levels. The sandy texture of the soil enables the development of *Callitris glauca,* a species which reaches its maximum development in this region on the deep sands and sandy loams of the alluvial and residual red-brown earths. In some places, e.g. on the western slopes of the Yambla Range, *C. calcarata* takes the place of *C. glauca. C. calcarata* is confined to the rocky outcrops of the ranges and does not occur on the red-brown earths.

In physiognomy and structure, the *E. dealbata-C. glauca* Association resembles the two preceding associations. *E. dealbata* rarely exceeds 30 ft in height and *C. glauca* and *C. calcarata* are commonly the tallest species in the tree stratum. Associated shrubs are rare, and the herbaceous stratum is poorly developed. Where partial clearing has occurred, *Aristida jerichoensis* var.

subspinulifera may become well developed, especially towards the western boundary of the region. In other areas, the most common species in this stratum is *Stipa falcata*. Herbs and legumes are rare, and appear only in well-watered pockets. Annual species form a sparse covering for a brief period following a wet winter.

The *Eucalyptus dealbata-E. macrorrhyncha* Association (Plate 4, Fig. 2) and the *E. dealbata-E. sideroxylon* Association (Plate 5, Fig. 1) occupy the lower slopes of the hills on soils which are probably of mixed origin. There is no doubt that the development of the soils has been influenced by material brought down from higher levels either by water or by gravity, but they appear to be in part at least developed *in situ*. The two communities are similar in their soil and moisture requirements, except that the former is developed more frequently on soils derived from granite, while the latter is developed more commonly on sedimentary rocks. Temperature would also appear to play a part in the determination of the particular community developed, since *E. macrorrhyncha* is more at home in the cooler situations, while *E. sideroxylon* prefers the warmer.

The dominants in these two associations are taller than those of the preceding associations, reaching a height of 40-50 ft. Associated small trees are rare, but *Callitris glauca* may be present. There is usually a sparse shrub stratum, in which the following species are the most common: *Hibbertia linearis, Phyllanthus thymoides, Lissanthe strigosa, Brachyloma daphnoides*, and *Acacia buxifolia*. The herbaceous stratum is weakly developed and consists usually of a few widely spaced plants of *Stipa falcata* and *Danthonia* species, together with a few winter annuals. *Cheilanthes tenuifolia* is commonly present.

The *Eucalyptus sideroxylon* Association occurs on soils which are somewhat more developed than those of the previous types. The surface soil is usually deep and sandy, and the B horizon is commonly a yellow clay. This association is not widespread, as there are relatively few areas of suitable soil within the region and *E. sideroxylon* develops only in a relatively warm habitat. The trees tend to be slightly taller than in the two previous associations but the shrub and herbaceous strata are again weakly developed.

The *Eucalyptus sideroxylon-E. woollsiana* Association (Plate 5, Fig. 2) occurs on the lowest slopes of the hills, where the soils are commonly deepest and most mature, though in some areas they may contain a high proportion of undecomposed rock.

This community occurs in a position intermediate between typical areas of *E. woollsiana* Woodland on the one hand and *E. dealbata-E. sideroxylon* Dry Sclerophyll Forest on the other. From this point of view it might logically be regarded as an ecotone. It has been included in the *E. dealbata-E. sideroxylon* Alliance for the following reasons:

(1) The dominant stratum always includes a high proportion of *E. sideroxylon; E. woollsiana* may be co- or subdominant according to the soil conditions.

(2) The structure and physiognomy of the community are those of a forest, not a woodland; the trees have a forest form, reaching a

> height of perhaps 70 ft, there is a well-developed shrub stratum, and there is a poorly developed herbaceous stratum.

This association reaches its maximum development on the low ranges between Temora and Ardlethan and in the Temora-Cootamundra-Stockinbingal area. It has been observed in a number of areas to the north, notably between Dubbo and Tomingley, and has been described in Victoria by Patton (1944) as the Box-Ironbark Association.

Callitris glauca is a constant member of the communities studied. There is a well-developed shrub stratum, which includes a greater variety of shrubs than in any other association within the *E. dealbata-E. sideroxylon* Alliance. Tall shrubs are rare but small shrubs are common and include *Acacia flexifolia, A. buxifolia, A. difformis, A. hakeoides, A. leprosa, A. verniciflua, A. viscidula, Fusanus acuminatus, Cassinia aculeata, C. arcuata, Casuarina paludosa, Myoporum deserti, Helichrysum semipapposum, H. obcordatum, Grevillea lanigera, Pultenaea foliolosa, Dillwynia floribunda, Hibbertia linearis, Brachyloma daphnoides, Phyllanthus thymoides, Lissanthe strigosa.* The herbaceous stratum is poorly developed, but commonly includes *Stipa falcata, Danthonia* spp., *Goodenia glabra, G. hederacea, Helipterum australe, Cheilanthes tenuifolia,* and *Stuartina muelleri.*

The *Eucalyptus sideroxylon-E. polyanthemos* Association was included by Pidgeon (1942) as a type of the *E. macrorrhyncha-E. rossii* Association (as defined by Pryor 1939), but it is here included in the *E. dealbata-E. sideroxylon* Alliance since it is considered that it is more closely related to the latter than to the former. It is of relatively minor importance, being found generally as a marginal community of small extent. It does not extend far to the west, since *E. polyanthemos* is apparently not capable of withstanding the hot, dry conditions. Nevertheless, since both dominants prefer relatively warm situations and deep soils, it is most commonly found at the bottom of the warmer slopes in the areas of higher rainfall. It develops in topographic situations similar to those of the *E. sideroxylon-E. woollsiana* Association. Shrub development is poor, but there is usually a more strongly developed herbaceous stratum than in the other associations of this alliance, and reasonably good *Stipa-Danthonia* pastures may develop after clearing.

Acacia baileyana occurs in the Dry Sclerophyll Forest communities in the Temora-Cootamundra-Stockinbingal district (Plate 6, Fig. 1). This species was widely planted as an ornamental before any records of its natural occurrence were made, and in some areas it rapidly became naturalized. There has therefore been some doubt as to its natural habitat and distribution. Newman (1935), after examination of the available evidence, concluded that *A. baileyana* is "a species occurring naturally in a restricted habitat at localities within about 20 miles of Cootamundra and Temora." It occurs in situations sheltered from the south-west and generally, though not invariably, towards the highest ground.

(ii) *Eucalyptus macrorrhyncha-E. rossii Alliance.*—This alliance has been described by Pryor (1939) for the Australian Capital Territory and by Costin (1952) for the Monaro Region, where it reaches maximum development. In the regions studied it reaches its western limits, and is confined to certain more or less specialized habitats where the mean annual rainfall is over 23 in. Within this zone it develops on immature and skeletal soils of the southern and eastern slopes of the ranges. No well-developed stand with a typical shrub stratum has been observed.

Though the soils are less well developed than the red and yellow podsolic soils of the neighbouring *E. albens* Alliance, they have in general reached a more advanced stage of development than typical soils within the *E. dealbata-E. sideroxylon* Alliance. The major factors responsible for this more advanced soil development are:

(1) The slopes of the southern and eastern aspects are in general much more gentle than those of the northern and western aspects, thus providing more favourable conditions for the accumulation of soil.

(2) The relatively high rainfall, combined with the greater moisture penetration on the gentler slopes, allows of more rapid leaching of the surface soils and the development of illuvial horizons.

Numerous stands of the *E. dealbata-E. sideroxylon* Alliance occur within the area where the *E. macrorrhyncha-E. rossii* Alliance is found, and it has not been possible to map accurately the distribution of the two communities. The former alliance is confined chiefly to the warmer and drier sites (northern and western slopes) while the latter is confined chiefly to the cooler and moister sites (southern and eastern slopes). In intermediate areas there is a mingling of the dominants of both communities, and it is impossible to draw a dividing line between them.

Five associations have been recognized, viz. *Eucalyptus rossii, E. macrorrhyncha-E. rossii* (Plate 6, Fig. 2), *E. macrorrhyncha-E. maculosa, E. macrorrhyncha-E. polyanthemos*, and *E. macrorrhyncha-E. elaeophora* (Plate 7, Fig. 1). In all of these associations the shrub stratum is sparse or lacking. Shrubs most commonly found include *Acacia buxifolia, A. decurrens, A. diffusa, Daviesia latifolia, Hibbertia linearis, Brachyloma daphnoides, Lissanthe strigosa, Melichrus urceolatus, Stypandra glauca.* There are few trees other than the dominants of the communities, the only one of more than rare occurrence being *Exocarpus cupressiformis.* The herbaceous stratum is generally poorly developed or absent, and consists chiefly of a few scattered perennial grasses (*Stipa* and *Danthonia* spp.). It is frequently fairly well developed in the *E. macrorrhyncha-E. polyanthemos* Association, which closely approaches woodland in structure and physiognomy.

The *Eucalyptus rossii* Association has been observed in two places only on low ranges of a very deep residual sand, apparently derived from sandstone. Either leaching has been excessive or no clay-forming minerals were present in the parent material, since no illuvial horizon was found on boring to a depth of 3 ft. The occurrence of the community in these places would appear to be related to the fact that the deep sandy soil allows of ready penetration of water, and that the water is readily available to the plants.

(c) *Swamp Sclerophyll Forest*

Swamp Sclerophyll Forest is a sclerophyll forest characterized by a herbaceous stratum of helophytes.

The *Eucalyptus camaldulensis* Alliance may occur within this subformation. However, the structure of communities having *E. camaldulensis* as the dominant varies from savannah woodland to forest and within the region it is most frequently seen as a woodland. It will therefore be described under the latter heading.

(d) *Tall Woodland*

Tall Woodland is a closed community characterized by a tall, sparsely continuous dominant stratum of mesophanerophytes in which the crown depth is equal to or only slightly greater than the length of the bole. There is a poor development or lack of subordinate shrub and herbaceous strata. The trees may reach a height of 80 ft in the more favourable situations.

Tall Woodlands occupy from one-half to three-quarters of the region, both on the red-brown earths and on the deeper red and yellow podsolic soils.

(i) *Eucalyptus woollsiana* Alliance.—This extends westwards from about the 24-in. to about the 15-in. isohyet. It occurs as far north as Gilgandra and possibly further, but is confined essentially to the southern (winter-rainfall) part of New South Wales. It occurs also in northern Victoria (e.g. the Goulburn Valley and along the Murray Valley from Corowa to the west of Cobram) on the red-brown earths.

Within its climatic limits, *E. woollsiana* occurs on the red-brown earths or closely related soils, and in general there is a sharp boundary between this alliance and the *E. albens* Alliance, which occurs on the red and yellow podsolics or the basaltic chocolate soils of the western slopes. Towards the lower limit of rainfall *E. woollsiana* becomes more and more closely confined to the deep, sandy soils, e.g. to the south-west of Deniliquin.

The *E. woollsiana* Alliance is typically a Tall Woodland, though in the drier districts it tends to assume a Savannah Woodland form. In well-developed stands in the higher-rainfall areas the trees may reach a height of 70-80 ft. A number of scattered shrubs occur throughout the alliance but are usually not of sufficient frequency to form a definite stratum. However, in the northern part of the region and towards the western limits of the alliance a shrub stratum may be present.

Four associations have been recognized within this alliance, viz. *Eucalyptus woollsiana, E. woollsiana-C. glauca, E. melliodora-C. glauca,* and *E. woollsiana-E. populifolia.* The latter association occurs only in limited areas near Ardlethan at the southern and eastern limits of distribution of *E. populifolia,* and will not be considered in detail.

The *Eucalyptus woollsiana* Association (Plate 7, Fig. 2) is found chiefly on the heavier-textured red-brown earths, the most typical examples being seen in the northern portion of the region to the north of Stockinbingal, and between Wagga and Narrandera. Typical stands of the association have occasionally been observed on soils other than red-brown earths, but such occurrences are rare. A narrow strip on the outskirts of the Bullenbung Plain (between Wagga and Lockhart) consists of a heavy self-mulching grey clay (belonging to the grey and brown soils of heavy texture), and here a typical stand of the *E. woollsiana* Association occurs. It also occurs on a small area of a podsolized soil between Culcairn and Walbundrie.

The structure and physiognomy of the community are those of a Tall Woodland, with few or no small trees and shrubs. *Callitris glauca* may be present as a rare or occasional species, but is frequently absent. The most commonly occurring shrubs are *Acacia buxifolia* and *Dodonaea cuneata*. In the undisturbed condition the herbaceous stratum is discontinuous, consisting chiefly of scattered perennial grasses (*Danthonia* spp. and *Stipa falcata*) with a few perennial herbs (*Sida corrugata, Euphorbia drummondii, Oxalis corniculata*). Where moisture supply is adequate during winter and spring, annual herbs may appear, together with a few annual grasses.

The *Eucalyptus woollsiana-Callitris glauca* Association (Plate 8, Fig. 1) is widespread and occupies a greater area than any of the other associations within the *E. woollsiana* Alliance. It is found in the greater part of the County of Denison, chiefly on light-textured alluvial soils, on the residual soils derived largely from sandstones in the counties of Urana, Mitchell, and Bourke, and in the western part of the County of Hume on alluvial soils. It is always associated with a soil containing a high percentage of sand in the A horizon, textures ranging from sands to sandy loams. Except in the higher-rainfall areas (above 18 in. per annum) alluvial soils with a shallow A horizon (less than 3-4 in.) will not support any association within the *E. woollsiana* Alliance even though the surface soil may be of a light texture. On these soils *A. pendula* becomes the dominant species.

The structure and physiognomy are those of a tall woodland, with *E. woollsiana* attaining a height of 70-80 ft. *C. glauca* grows in greater or less density according to the texture of the soil, being most abundant on the deep sands. Its height varies from 40 to 60 ft, and it seldom, if ever, reaches the full height of the *E. woollsiana*. *Casuarina luehmannii* is frequently seen as a subsidiary species in the tree stratum. It does not appear to have any marked soil preferences. On many of the residual soils *Brachychiton populneus* may be common.

The density of the shrub stratum varies considerably, but in no stand has a continuous shrub stratum been observed. There is a tendency for an increased development of shrubs and small trees in the warmer and drier areas, perhaps because of the decreasing density of the dominants. In a stand examined about 20 miles south of Darlington Point (to the west of the area surveyed) the following species were observed growing commonly: *Heterodendron oleifolium, Geijera parviflora, Acacia oswaldii, Pittosporum phillyraeoides, Acacia salicina, Hakea leucoptera, Eremophila longifolia, Cassia eremophila,* and less commonly *Exocarpus aphylla, Jasminum lineare,* and *Fusanus acuminatus.* Within the area surveyed, none of these species is common but the following may be found occasionally, especially towards the western boundary: *Heterodendron oleifolium, Pittosporum phillyraeoides, Hakea leucop-*

tera, Acacia salicina, and *A. oswaldii* (Plate 9, Fig. 1). The only commonly occurring tall shrub in the region studied is *Acacia decurrens.* Small shrubs (less than 6 ft) occur throughout the association, but tend to be more common to the north of the area than in the south. The most common species include *Acacia buxifolia, A. hakeoides, A. difformis, A. montana, A. verniciflua, Myoporum deserti,* and *Dodonaea cuneata.*

The herbaceous stratum is poorly developed, consisting chiefly of scattered plants of *Stipa falcata* and *Danthonia* spp. together with occasional annual and perennial herbs such as *Sida corrugata, Euphorbia drummondii, Oxalis corniculata, Goodenia* spp., *Crassula sieberiana, Stuartina muelleri,* and *Brachycome* spp.

The *Eucalyptus melliodora-Callitris glauca* Association (Plate 8, Fig. 2) occurs on deep, sandy soils (usually sandhills of aeolian or alluvial origin), or as small, localized areas on shallower or heavier-textured soils at relatively low levels where the moisture supply is augmented by run-off from the surrounding country, and where there is good drainage. It may also occur on deep, sandy soils derived from sandstone, e.g. between Morundah and Boree Creek. On the sandhills *C. glauca* is a prominent species, its density in these situations being similar to that within the *E. woollsiana-C. glauca* Association. In the second kind of habitat referred to above, *C. glauca* is much less prominent and may even be absent. This association has been observed on sandhills as far west as the Bublebundie Sandhill about 25 miles south-west of Darlington Point. In structure and physiognomy it closely resembles that of the *E. woollsiana-C. glauca* Association, and the shrub and herbaceous strata are similar.

(ii) *Eucalyptus albens* Alliance.—The *E. albens* Alliance is found on the red and yellow podsolic soils, chiefly to the east of the 19-in. isohyet. The complete range of this alliance has not yet been determined, but it extends some distance to the east of the region studied, its limits in this direction possibly being determined by temperature (Cambage 1904, 1907). Well-developed stands occur on the Southern Tablelands between Yass and Wee Jasper. It has been recorded by Costin (1952) as the *E. albens-C. glauca* Alliance in the Jacob's River area in the southern part of the Monaro region, from there extending across the border of New South Wales into Victoria. It occurs also on the central-western and north-western slopes where it has been observed by the author as far north as Gunnedah. Blakely (1934) states that *E. albens* occurs as far north as Inverell and Narrabri, with a limited occurrence in southern Queensland. The species has been observed by the author in some parts of northern Victoria (e.g. Chiltern and Cobram). It is recorded by Blakely (1934) in a few other areas in Victoria. In southern New South Wales its western limit is between Corowa and Mulwala, near the Murray River.

Eucalyptus albens shows relatively little preference for any particular soil type within its climatic limits, but is not generally found on the red-brown earths. Occasional trees occur in the higher-rainfall areas, but this species is apparently unable to compete successfully with *E. woollsiana* on these soils. Good stands are found on podsolic soils derived from granites, sedimentary rocks (sandstones, shales, etc.), and on gneissic formations, as well as on the reddish chocolate soils derived from basalt. In other areas it has been observed on soils derived from andesite and various calcareous and non-calcareous sedimentary rocks (Cowra-Woodstock district). Between Yass and Wee Jasper the soils are red and yellow podsolics, and terra rossas derived from limestone.

The topography of the country occupied by the *E. albens* Alliance is undulating to hilly, intersected by many watercourses, both temporary and permanent.

The structure and physiognomy are typically those of a tall woodland, varying to a savannah woodland in the least favourable sites, notably the shallow and skeletal soils associated with rocky outcrops at or near the tops of the hills. The trees reach a maximum height of 70-80 ft. The canopy is never completely closed, but is more open in areas having a savannah woodland form than in those with a tall woodland form. Associated trees include *E. melliodora, E. blakelyi, E. stuartiana, E. macrorrhyncha, Brachychiton populneus, Callitris glauca, Casuarina stricta,* and *Acacia implexa. E. melliodora* and *E. blakelyi* may become locally dominant along non-permanent watercourses and on the deeper and more highly leached podsolic soils of the valleys. *E. stuartiana* is generally confined to the best-watered sites close to the watercourses. These local communities in the more favourable habitats are numerous throughout the association, but almost always have associated with them well-developed *E. albens* as a co- or subdominant (it has almost certainly been cleared from areas where it does not occur at the present day). They are therefore regarded as an association closely related floristically to the *E. albens* Association and hence included in the same alliance, the change in the dominants being brought about by a more favourable local environment. It should be noted, too, that both *E. melliodora* and *E. blakelyi* occur as occasional species in the *E. albens* Association, there being a gradual increase in these two species as one moves from the top to the bottom of a slope. It would be difficult, if not impossible, to draw a sharp line between the two communities.

Probably because of this constant development of *E. melliodora* and *E. blakelyi* in the most favourable situations, Pidgeon (1942) suggested that the woodlands of the slopes and tablelands be included in one association (=alliance) which she named the *E. albens-E. melliodora-E. blakelyi* Association. Pryor (1939) described the *E. melliodora-E. blakelyi* Savannah Woodland in the Australian Capital Territory, and Costin (1952) has mapped the same community in the Monaro Region. It is considered that two alliances should be recognized because *E. albens* does not occur in the *E. melliodora-E. blakelyi* communities of the Tablelands, the *E. albens* communities are typically tall woodlands whereas the Tableland communities are typically savannah woodlands, and the moisture and temperature requirements of the two alliances appear to differ markedly.

Brachychiton populneus appears chiefly in the more rocky areas where the soil is shallow and the habitat is the driest for the whole alliance. *E. macrorrhyncha* becomes codominant in some areas of relatively high rainfall. *C. glauca* may be a co- or subdominant on sandy soils towards the western limits of the alliance.

Four associations are recognized according to the dominant species in the several communities, viz. *E. albens, E. albens-E. macrorrhyncha, E. albens-C. glauca,* and *E. albens-E. melliodora-E. blakelyi.*

The *Eucalyptus albens* Association (Plate 9, Fig. 2) is the most widespread, and occurs principally on what may for convenience be termed the "normal" soils, i.e. they are generally deep and well-developed red and yellow podsolics. The community is typically a tall woodland, varying to a savannah woodland in the least favourable habitats.

In this community there is a single dominant (*E. albens*) with few or no associated trees and shrubs. *Brachychiton populneus* may be common on the more rocky sites, and on some hills *Casuarina stricta* may be a prominent member of the community. *Acacia implexa* may occur as an occasional small tree. Though shrubs are rare and do not form a well-developed stratum, a number are met with fairly frequently, at least on roadsides, if not in grazed areas. These include *A. buxifolia, A. armata, A. pycnantha, Dodonaea cuneata,* and *Bursaria spinosa.*

The herbaceous stratum is well developed. Sturt (1834) mentions the good grazing in this community, referring more especially to what he called "forest grass." This term was probably used in reference to more than one species of tall tussock grass. The evidence of exclosures suggests that the original dominant in the herbaceous stratum may have been *Themeda australis,* with *Poa australis* and *Stipa aristiglumis* as subdominants in the wetter areas. None of these species can withstand heavy grazing by sheep and is seldom seen in grazed areas (see also Andrews 1920). They are generally present in more or less protected areas such as cemeteries, railway embankments, and little-used stock routes. It is unlikely that any evidence will be found to provide definite proof as to whether these species were those referred to by Sturt as "forest grass," but it may be concluded that a herbaceous stratum dominated by these grasses would be more nearly representative of the original conditions than the pastures of the disclimax communities. Under grazing, the dominant species of the herbaceous stratum are *Stipa falcata* and *Danthonia* spp. Other common species include *Panicum effusum, Chloris truncata, Sida corrugata, Euphorbia drummondii, Oxalis corniculata, Solenogyne bellioides* var. *gunnii, Goodenia pinnatifida, Velleia paradoxa, Helichrysum apiculatum, Vittadinia triloba, Aristida behriana,* and *Agropyron scabrum. Dianella laevis* occurs commonly on roadsides and railway embankments but is not found in grazed areas.

The *Eucalyptus albens-E. macrorrhyncha* Association may be either of the nature of an ecotone between *E. albens* and one of the Dry Sclerophyll Forest communities or a marginal community. Since, however, there are fairly extensive tracts of this community, especially in the higher-rainfall areas, and since its structure is typically that of a tall woodland rather than that of a forest, it is included in the *E. albens* Alliance. It is similar to the *E. albens* Association in structure and physiognomy.

There is a poorly developed shrub stratum, the most common species including *Lissanthe strigosa, Acacia buxifolia,* and *Hibbertia linearis.* The herbaceous stratum is similar to that of the *E. albens* Association, except that

Aristida ramosa may be present, especially on sandy soils derived from granite, and the herbaceous stratum is less well developed.

The *Eucalyptus albens-Callitris glauca* Association (Plate 10, Fig. 1) occurs only on deep, sandy soils in a few localities towards the western boundaries of the alliance. Shrubs are rare, and the herbaceous stratum less well developed than in other associations, probably because of the shading effect of the *Callitris*. This association also occurs on the eastern side of the Dividing Range in the Monaro region of New South Wales, and extends into Victoria. It has been described for this area by Costin (1952).

The *Eucalyptus albens-E. melliodora-E. blakelyi* Association (Plate 10, Fig. 2) is confined to the most favourable habitats where the moisture supply is greatest, usually at low levels where additional water is received as run-off from higher levels. The soils in such situations are more highly leached than those on the slopes of the hills, as indicated by the colour of the A horizon and the lower percentage of iron in the surface. The association may also occur on deep, sandy soils at relatively high levels, as may be seen to the north of Old Junee. In structure and physiognomy it resembles the *E. albens* Association except that it less frequently takes the form of a savannah woodland, and shrubs are less common. Because of the more favourable moisture relations there is a greater percentage of exotics (especially annual grasses and legumes) in the herbaceous stratum of the disclimax.

(*e*) *Savannah Woodland*

Savannah Woodland is an open community characterized by a discontinuous dominant stratum of mesophanerophytes with rounded crowns, separated by a distance equal to or slightly greater than the diameter of the crown. There is usually a continuous herbaceous stratum. Shrubs are frequently found, but do not form a definite stratum.

The savannah woodlands include the *E. largiflorens* Alliance, a large proportion of the *E. camaldulensis* Alliance, and some portions of the *E. albens* Alliance (see previous section).

(i) *Eucalyptus largiflorens* Alliance (= *E. bicolor* Association of Beadle (1948)).—This alliance consists of one association only, chiefly in the Western Division of New South Wales, and within the region studied there is only a small area to the west of Jerilderie (Plate 11, Fig. 1). It occurs on low-lying areas of heavy grey soil subject to infrequent flooding. It is a typical savannah woodland with an open canopy, allowing the development of a continuous cover of herbaceous plants. The shrub stratum is lacking although in its more typical development further west shrubs may be common (Beadle 1948). However, it appears probable that various shrub species of *Atriplex* were present in the original community. Probably the most abundant species in the herbaceous stratum is *Kochia ciliata*.

For a detailed account of the typical community and its soils, reference should be made to Beadle (1948). Some inaccuracies in the distribution of this association as shown by Beadle require mentioning. It does not occur along Yanko Creek between the Murrumbidgee River and the western boundary of the County of Urana. The flood plains of this creek are occupied by *E. camaldulensis*, and are intersected at intervals by sandhills carrying *E. woollsiana* Alliance. To the west of Yanko Creek, on both sides of the Murrumbidgee, the large area shown by Beadle as *E. bicolor* Association is, in fact, a complex mosaic including three associations. The *E. largiflorens* Association occupies the heavy grey soils of the depressions, while *Acacia pendula-Atriplex nummularia* Alliance occurs on the red-brown earths at slightly higher levels, and on the grey and brown soils of heavy texture. On deep sandy soils the *E. woollsiana* Alliance is found. Of these communities, *E. largiflorens* is probably the least extensive. In the south-east corner of the County of Townsend, the area shown by Beadle (1948) as the *E. bicolor* Association is again a complex of the same three communities, their distribution being determined by the soil types.

(ii) *Eucalyptus camaldulensis Alliance.*—Only one association within this alliance occurs in the region, viz. the *E. camaldulensis* Association, although Beadle (1948) includes a second, the *E. ochrophloia* Association. This alliance occurs in two distinct structural forms according to the habitat. On the lower reaches of the Murray (west of Mulwala) and Murrumbidgee rivers (west of Wagga) well-developed forest communities occur, but on the upper reaches of these two rivers (e.g. at Albury and Gundagai) the community has the structural form of a savannah woodland (Plate 11, Fig. 2). The savannah woodland form is seen also along many of the smaller streams (Plate 12, Fig. 1) and in a few small areas subject to inundation. Extensive areas of savannah woodland in which *E. camaldulensis* is the dominant are found in the south-east of South Australia and in western Victoria. Beadle (1948) has described the forest form of this community as it occurs on the Murray River to the west of Tocumwal.

The association occurs on a wide range of soils, but since it is found near watercourses and in areas subject to inundation, it commonly occurs on heavy grey soils. However, the soils vary from sands, as in some areas along Yanko Creek, to heavy clays. Downes (1947) examined the soils in two areas of the *E. camaldulensis* Association on the Murray River. The soils are alluvial deposits developed on a variety of parent materials, and since they are subject to frequent inundation (often with deposition of new parent material) they are in general immature, and within a small area numerous soil types may be present.

No associated tree species have been observed in the *E. camaldulensis* Association, and only one shrub species, *Acacia decurrens*, which occurs commonly in a thinned stand near Barooga. As Beadle (1948) pointed out, the development of the herbaceous stratum depends on the degree of clearing and subsequent treatment. The most commonly occurring species are *Hordeum leporinum, Bromus rigidus, B. mollis, Vulpia bromoides, Danthonia* spp., *Trifolium glomeratum, Medicago denticulata, Erodium moschatum*, and in the more swampy areas *Amphibromus neesii.*

This community is shown on the vegetation map only along the Murray and Murrumbidgee Rivers and along Yanko Creek, where fairly extensive areas occur. Other stands are too small to show on the map, but it occurs along all creeks and watercourses within the *E. woollsiana* and the *Acacia pendula-Atriplex nummularia* Alliances, and most of the permanent streams within the *E. albens* Alliance.

(*f*) *Shrub Woodland*

Shrub Woodland is an open woodland community characterized by a discontinuous dominant stratum in which the crowns of the dominants are separated by a distance greater than the diameter of the crown, a discontinuous but well-developed shrub stratum, and a continuous or discontinuous herbaceous stratum.

Only one alliance within this subformation occurs within the region, viz. the *Acacia pendula-Atriplex nummularia* Alliance in which one association only is represented. It seems probable from observation in other areas that there is a second association in this alliance in which the dominant is *Acacia pendula* with no *Atriplex nummularia*.

The *Acacia pendula-Atriplex nummularia* Alliance (Plates 12-15) extends westwards from about the 18-in. isohyet, and in the region studied is confined chiefly to the County of Urana, with some smaller areas in the counties of Mitchell, Denison, Hume, Cooper, and Bourke. Beadle (1948) has described and mapped this community to the west of Yanko Creek as the *Chloris-Danthonia* Association, but the grassland form is that of the disclimax induced by clearing and grazing of the original dominants (see Section IV (*a*)). It appears probable that the western boundary of the alliance is somewhat to the east of that shown by Beadle (1948) for the *Chloris-Danthonia* grassland, but its precise limits have not been determined.

Two major groups of soils occur within the area occupied by this alliance, the red-brown earths and the grey and brown soils of heavy texture. The topography is flat, but minor topographic differences are associated with major soil changes, the grey and brown soils of heavy texture occupying the lower and less well-drained sites. These grey and brown soils frequently have a self-mulching surface, when gilgais are usual, but soils with a compact surface and no gilgai formation are not uncommon. The texture varies from a clay loam to a heavy clay. The red-brown earths are generally sandy loams to loams with a shallow A horizon (3 in. or less) and a typical clay B horizon.

There is considerable difficulty in reconstructing a picture of this alliance, since there is no stand where the original structure has not been considerably modified by grazing and removal of the dominant species. Further, many species originally present in the lower strata have no doubt disappeared and have been replaced by a number of exotic species. East of Yanko Creek no old stand of *Acacia pendula* has been observed, but to the west of Yanko Creek there are extensive areas where the trees have not been completely removed, and some idea of the original physiognomy can be obtained (Plate 12, Fig. 2). Trees up to 30 ft are common, and it would appear that the community was an open woodland, almost certainly with a well-developed shrub stratum consisting principally of *Atriplex nummularia*. Isolated old trees of the same habit can occasionally be seen east of Yanko Creek. Although there is considerable variation in the structural form of this alliance, it is considered that in its most typical form it is a shrub woodland, varying towards a shrub community where *Acacia pendula* becomes infrequent, and *Atriplex nummularia* is the dominant species.

The following description of the *Acacia pendula-Atriplex nummularia* Association is built up from the various sources of information given in Section IV(a). The association is regarded as a shrub woodland with a dominant tree layer of the order of 30 ft in height having an open canopy and a well-developed but probably discontinuous shrub stratum dominated by *Atriplex nummularia.* It would appear from the evidence that the dominant species on the red-brown earths was *Acacia pendula,* usually with a shrub stratum of *Atriplex nummularia,* while on the grey and brown soils of heavy texture the dominant species was *Atriplex nummularia,* with scattered trees of *Acacia pendula.* There were no other trees present, and associated shrubs included *Rhagodia spinescens, Enchylaena tomentosa,* and *Kochia aphylla,* and possibly a few other Chenopodiaceae. The herbaceous stratum was probably not well developed, the most likely common species including *Danthonia* spp., *Stipa falcata, Kochia excavata, Atriplex semibaccata,* and annuals such as *Helipterum* spp., *Isoetopsis graminifolia, Myriocephalus rhizocephalus,* and *Brachycome* spp. On the heavier-textured soils, especially those with a self-mulching surface, it is probable that *Stipa aristiglumis* and *Panicum prolutum* would also have been prominent members of the herbaceous stratum in addition to the species listed above.

IV. DISCUSSION

(a) *Evidence for the Climax Status of the* Acacia pendula-Atriplex nummularia *Alliance*

The evidence in support of the previous existence of the *Acacia pendula-Atriplex nummularia* Alliance in areas which are now almost entirely disclimax grasslands has been obtained from a variety of sources. It was clear from the beginning of the investigation that the *Chloris-Danthonia* and *Stipa* communities described by Beadle (1948) were disclimax communities. In his discussion on the status of these communities, Beadle refers to the evidence of some of the older inhabitants that saltbush once occurred there, but the evidence was meagre, and he preferred tentatively to regard the vegetation as being a true climax. Comparison of the species growing in this area under sheep-grazing with those in other areas, however, immediately suggests that the community is a disclimax, and further, that various degrees of degeneration are evident. *Chloris* spp. (especially *Chloris truncata*) are dominant only in areas subjected to more or less heavy grazing, while *Stipa falcata, S. variabilis,* and *Danthonia* species are not found as dominants except under grazing in any part of the south-east of New South Wales. Biddiscombe (1953) has shown that in the Trangie district *Chloris* species become dominant in the pastures only under relatively severe grazing. Further evidence is supplied by the frequent occurrence of *Stipa aristiglumis* (a tall grass) as the dominant in lightly grazed areas on the heavier-textured soils, and its occurrence as an occasional species in moderately grazed areas, as well as its frequent appearance as a minor species on many of the lighter-textured soils.

An attempt was made to interpret the disclimax communities on the assumption that the climax was in fact a grassland with *Stipa aristiglumis* as the probable dominant. A closer examination of the distribution of this species, however, revealed the fact that under light grazing it is abundant on the grey and brown soils of heavy texture, especially when the surface soil is self-mulching, but that it is never more than an occasional species on the red-brown earths, even under the most lenient of grazing treatments. Further, on the latter soils it grows to a maximum height of about 2-3 ft, in contrast to the very tall grass, up to 5 and 6 ft, seen on the heavy soils. A grassland community with *Stipa aristiglumis* as the dominant has been described for the Liverpool Plains and other districts (Beadle 1948), and an inspection of the communities in this area indicated that it would be difficult to show that the grasslands of the Riverina and those of the Liverpool Plains belonged to one association or even to one alliance. Further, the regeneration of *Acacia pendula* in areas protected from grazing for a number of years (Plate 13, Figs. 1 and 2) would be difficult to explain except on the assumption that this species was a dominant in the original community.

Relict stands of the *Acacia pendula-Atriplex nummularia* Alliance have been found on two stud Merino properties, "Coonong," 10 miles north of Urana, and "Coree," 11 miles west of Jerilderie. On both properties the stands containing *Atriplex nummularia* were originally the horse paddocks. Horses do not destroy this species, and sheep were excluded. During more recent years, carefully controlled sheep-grazing (with young sheep only) has been practised to avoid damage to the *Atriplex*. Rabbits, which cause extensive damage to the *Atriplex* spp., are virtually non-existent on these properties.

At "Coonong" two interesting relict areas occur. The first is on a medium-textured soil, and consists of a vigorous stand of *Atriplex nummularia* with scattered trees of *Acacia pendula* (Plate 14, Figs. 1 and 2). *Rhagodia spinescens* is the only other member of the shrub stratum. The herbaceous stratum is dominated by *Danthonia* spp., with introduced annuals, chiefly *Hordeum leporinum* and *Erodium cygnorum*, prominent during the winter. The other relict area occurs on old flood plains of a small creek. The dominant species is *Acacia pendula* with a shrub stratum of *Rhagodia spinescens*, and *Enchylaena tomentosa*. The herbaceous stratum consists of a sparsely developed *Danthonia* pasture with numerous endemic annuals and few introduced species.

At " Coree" the relict area containing saltbushes (Plate 15, Figs. 1 and 2) is somewhat different, owing to the fact that it is situated close to the Billabong and Yanko Creeks, and lies between a sandhill carrying *Callitris glauca* and *Cassia eremophila*, and a community of *E. largiflorens* at the lower levels nearer the creek. As a result of its proximity to *E. largiflorens*, the latter species occurs occasionally within the area dominated by *Acacia pendula* and *Atriplex* species. This area is of interest also because it is divided into two distinct parts, in one of which *Atriplex nummularia* is the only shrub, while in the other the most abundant shrub is *A. vesicaria* with scattered *A. nummularia*. Over the whole area the herbaceous stratum is similar, consisting chiefly of species of *Danthonia*, *Kochia*, *Helipterum* and other endemic and exotic annuals. A comparison of the species observed in the two areas at "Coonong" and the one area at "Coree" is given in Table 6.

TABLE 6

SPECIES IN RELICT SALTBUSH AREAS AT "COONONG" AND "COREE"

Species	"Coonong"	"Coree"	Species	"Coonong"	"Coree"
Eucalyptus largiflorens		x	*G. pusilliflora*		x
Acacia pendula	x	x	*Daucus glochidiatus*	x	x
A. oswaldii		x	*Sida corrugata*		x
Atriplex nummularia	x	x	*Spergularia rubra*	x	x
A. vesicaria		x	*Oxalis corniculata*	x	
A. semibaccata	x		*Bulbine bulbosa*	x	
Rhagodia spinescens	x	x	*Dichopogon strictus*	x	
Enchylaena tomentosa	x		*Haloragis* sp.	x	
Kochia aphylla		x	*Cryptostemma calendula*	x	
K. ciliata		x	*Salsola kali*	x	
K. excavata		x	*Lepidium fasciculatum*	x	
Bassia sp.		x	*Microseris scapigera*		x
Leptorrhynchus sp.		x	*Galium* sp.		x
Swainsona sp.		x	*Capsella bursapastoris*		x
Helipterum albicans		x	*Sonchus oleraceus*	x	x
H. variabile	x	x	*S. asper*		x
H. corymbiflorum		x	*Sisymbrium* sp.		x
Calotis scabiosifolia		x	*Medicago denticulata*	x	x
Minuria sp.		x	*Erodium cygnorum*	x	
Brachycome lineariloba		x	*Danthonia* sp.	x	x
B. marginata var.			*Stipa falcata*	x	x
chrysoglossa	x		*Vulpia bromoides*	x	x
B. marginata		x	*Bromus rubens*	x	x
Wahlenbergia sp.		x	*Hordeum leporinum*	x	
Crassula sieberiana	x	x	*Chloris acicularis*	x	
Plantago varia		x	*C. truncata*	x	
Goodenia sp.		x	*Lamarckia aurea*	x	

The relict areas at "Coree" and "Coonong" appear to be the only ones east of Yanko Creek in which *Atriplex nummularia* has been preserved. Stands of *A. nummularia* have until recently been maintained in the original horse paddocks on other properties to the west of Yanko Creek, but few of these have been preserved.

The evidence of the relict areas has been confirmed from a number of sources. Sturt's (1834) references to the vegetation of the plains near Narrandera suggest a mixture of *Acacia pendula* and saltbush (probably *Atriplex nummularia*). Townsend's maps of the Murrumbidgee River and of Billabong Creek were drawn in 1848 and show extensive areas of saltbush plain where disclimax grassland now occurs. Unfortunately his maps are confined to the country near the rivers, and no information about the intervening area can be gained from them. A map of the colony of New South Wales (Macdonald 1879) indicates extensive areas of saltbush plain over much of the country now appearing as grassland disclimax. Other documents showing the occurrence of saltbush include the maps prepared for the Pental Island Commission (Mitchell Library, Sydney).

The following extracts from the New South Wales Gazetteer (Anon. 1866) also corroborate the evidence from other sources:

> "Narrandera.—Surrounding country consists of saltbush and open boree [*Acacia pendula*] plains, with undulating sandhills at intervals. On the sandhills sparse pine and honeysuckle scrub [*Banksia marginata*]."
>
> "Jerilderie.—Surrounding country flat and thinly grassed, consisting of large open saltbush plains intersected by belts of myall [*Acacia pendula*] and box [*Eucalyptus woollsiana* and *E. largiflorens*]."

Still further valuable evidence on the original communities of the plains has been provided by Mr. C. R. Rawlins of "Uroly" Estate, near Narrandera. Mr. Rawlins's evidence has been most valuable since he can remember when the *Acacia* and *Atriplex* were the dominant species. His evidence supports the view that *Acacia pendula* was most prominent on the red-brown earths, and *Atriplex nummularia* most prominent on the heavy-textured soils, but that in fact both species grew in both situations. Apparently no other shrubby species of *Atriplex* (such as *A. vesicaria*) occurred, except possibly in some small areas. No doubt, too, this species would become gradually more prominent to the west, finally becoming the dominant species, with *A. nummularia* becoming more and more confined to the better watered areas. The disappearance of *Acacia pendula* and *Atriplex nummularia* is attributed primarily to the severe drought about 1875-77. Much of the *Atriplex* would have been eaten out by sheep prior to this date, but during the drought period the destruction of this species (except in the horse paddocks, which were never grazed by sheep) was completed. When all feed had been eaten it appears that the *Acacia pendula* was indiscriminately felled over large areas for stock feed. In the presence of grazing stock regeneration of this species is impossible. The complete disappearance of the logs and stumps (the wood is very hard and durable, and if left lying in the paddocks would not yet have rotted away) is attributed by Mr. Rawlins to the use of the timber for firewood and to bush fires.

Beadle (1948) has described the *Acacia pendula* community as an associes within the *Eucalyptus populifolia-Callitris glauca* Shrub Woodland subformation, although many stands occur far to the south and east of the limits of *E. populifolia*. He states that it "is invariably associated with heavy clay loams or clays (frequently self-mulching)." In the lower-rainfall areas (e.g. to the west of Deniliquin) it is true that this community is confined to the heavy soils, but within the region studied it occurs commonly on sandy loams and loams of the red-brown earth group, provided the surface soil is not deep. It would appear that, as the limits of rainfall for *Acacia pendula* are approached, the species becomes confined to the heavier-textured soils of high water-holding capacity, and receiving some run-off from higher levels. Many of these areas, too, are subject to winter flooding from nearby creeks.

Beadle's classification of this community as an associes depends on his observation that it occurs only on the heavy-textured soils, which he regarded as immature soils for the region. It is of interest to point out at this stage that Beadle (1948, p. 150) states that *Atriplex nummularia* originally played an important role as a fodder species, but that in most areas this plant has been completely removed, though a few good stands can still be found in the County of Clyde.

(*b*) *Relationships between Vegetation and Climate*

Because of the interaction between soil and climate there is usually no marked relationship between climate and vegetation, while relationships between soil and vegetation are more obvious. When one considers the distribution of individual species of *Eucalyptus* in relation to rainfall, however, some broad correlations can be determined. The distribution of the species occurring within the region in relation to rainfall is shown in Figure 8. Some species (*E. woollsiana, E. melliodora, E. dealbata, E. sideroxylon,* and *E. macrorrhyncha*) are found over the whole range of mean annual rainfall (15-27 in.), although each shows a preference for either the drier or wetter end of the range. Other species (*E. populifolia* and *E. largiflorens*) occur only towards the drier limits, while a third group (*E. albens, E. blakelyi, E. polyanthemos, E. maculosa,* and *E. rossii*) is confined to the higher-rainfall areas.

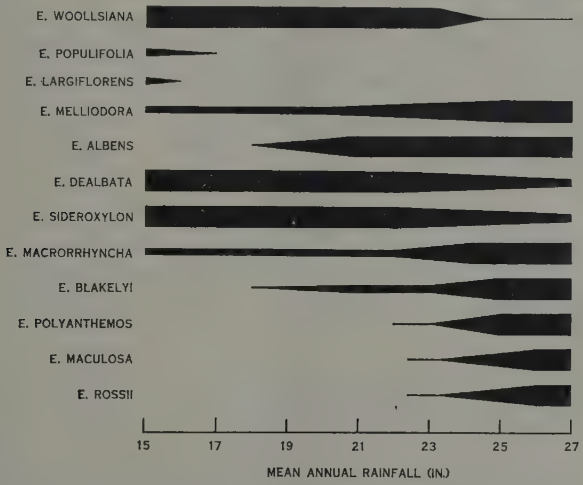


Fig. 8.—Distribution of *Eucalyptus* species in the south-eastern Riverina in relation to rainfall.

Similar correlations between rainfall and other groups of species could be determined. There are those (e.g. species of *Stipa* and *Danthonia*, many of the native and introduced annuals, some geophytes, and some hemicryptophytes) which occur over the whole range of rainfall conditions, those which are found only in the drier areas (e.g. *Atriplex* spp., *Kochia* spp., *Bassia* spp., etc.), and a third less well-defined group (e.g. *Acacia obliqua, A. pycnantha, A. rubida, Sebaea ovata, Brunonia australis,* etc.) members of which occur only in the areas of relatively high rainfall.

The influence of other climatic factors on the distribution of plants is also noticeable, but few quantitative measures of the factors involved are available and only approximate relationships can be determined. The effect of temperature on the distribution of *E. albens* has been discussed by Cambage (1904, 1907). This species occurs principally on the Western Slopes from the north to the south of New South Wales, but commonly reaches considerably higher elevations in the north than in the south. There is, in general, an increase in temperature as rainfall decreases and it is probable that with many species confined to the drier areas, the relatively high temperatures may be more significant than the low rainfall.

Some plants (e.g. *Muehlenbeckia* spp., *Eragrostis australasica, E. camaldulensis,* and *E. largiflorens*) occur in low-rainfall areas, but in habitats subjected to frequent flooding. Such species apparently require a high level of moisture supply either at some critical stage (e.g. *E. camaldulensis* for seed germination) or throughout their life cycle. Although the plants require a high level of moisture, rainfall is not the limiting factor. Other possible limiting factors are temperature, soil salinity, and the length of time during which the soil is saturated.

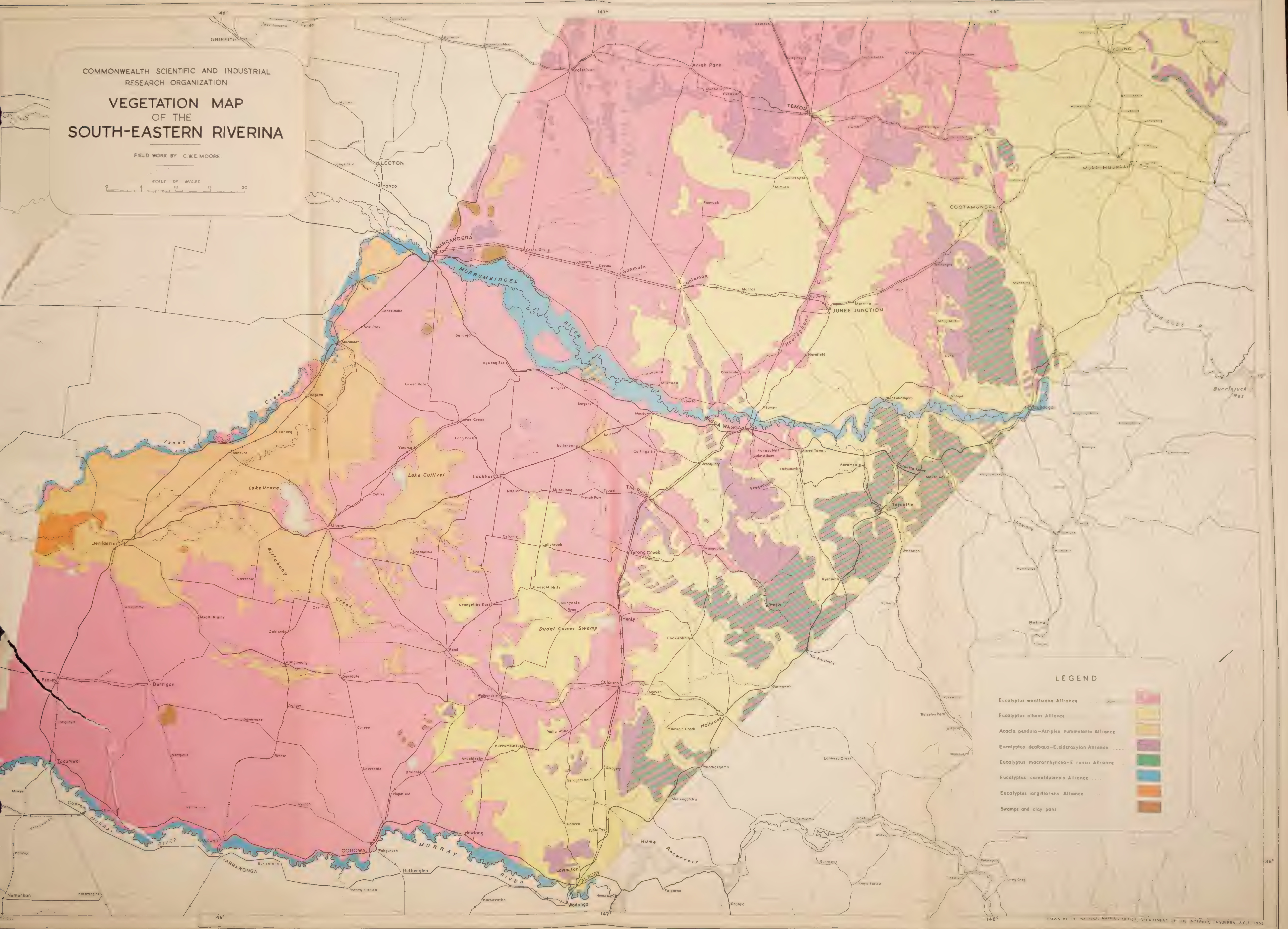
(*c*) *Relationships between Vegetation and Geological Formations*

There is little correlation between vegetation and geological formation. The *Eucalyptus albens* Alliance appears to develop equally well on soils derived from granites, basalt, and sedimentary rocks, as well as various kinds of metamorphic rocks; the *E. woollsiana* Alliance occurs on soils derived from Ordovician, Silurian, and Devonian sediments and on the alluvial soils of the plains. The dry Sclerophyll Forests occur more commonly on sedimentary rocks, though they are also to be seen on granites, especially where the soils are shallow.

This poor correlation between vegetation and geological formation appears to be due in large measure to the fact that different rocks give rise to soils which are similar in texture, reaction, and content of available plant nutrients.

(*d*) *Relationships between Vegetation and Physiography*

The difference in altitude between the highest and lowest points within the region is less than 2,000 ft. There is therefore no direct correlation between altitude and vegetation such as can be seen in alpine regions. Both *E. albens* and *E. woollsiana* communities may occur in similar topographic situations, but the former is confined to the podsolized soils and red loams and the latter, with minor exceptions, to the red-brown earths. Changes in the vegetation frequently occur in association with topographic changes, but are related to the corresponding soil changes rather than to differences in altitude *per se*. When topographic variations bring about marked changes in soils or in water relations, corresponding changes in the vegetation occur; but where no change or only a minor change in the soil occurs with change of topography, the vegetation remains constant. Such changes of soil and vegetation with topography are discussed in the subsequent Section.



COMMONWEALTH SCIENTIFIC AND INDUSTRIAL
RESEARCH ORGANIZATION

VEGETATION MAP
OF THE
SOUTH-EASTERN RIVERINA

FIELD WORK BY C.W.E. MOORE.

SCALE OF MILES

LEGEND

Eucalyptus woollsiana Alliance	🟥
Eucalyptus albens Alliance	🟨
Acacia pendula–Atriplex nummularia Alliance	🟧
Eucalyptus dealbata–E. sideroxylon Alliance	🟪
Eucalyptus macrorrhyncha–E rossii Alliance	🟩
Eucalyptus camaldulensis Alliance	🟦
Eucalyptus largiflorens Alliance	🟧
Swamps and clay pans	🟫

146°
147°
148°
36°
GRIFFITH
Yenda
LEETON
Yanco
NARRANDERA
Grong Grong
Matong
Ganmain
Coolamon
Ardlethan
Ariah Park
TEMORA
YOUNG
MURRUMBURRAH
COOTAMUNDRA
JUNEE JUNCTION
Old Junee
Morrar
Sebastopol
MURRUMBIDGEE RIVER
Houlaghans Ck
WAGGA WAGGA
Gundagai
Burrinjuck Res
Forest Hill
Lake Albert
Alfred Town
Ladysmith
Tarcutta
Mount Adrah
Morundah
Bundure
Coonong
Yanko Creek
Lake Urana
Lake Cullivel
Urana
Jerilderie
Lockhart
Billabong Creek
The Rock
Yerong Creek
Mangoplah
Pleasant Hills
Henty
Dudal Comer Swamp
Culcairn
Holbrook
Walla Walla
Burrumbuttock
Brocklesby
Gerogery
Jindera
Table Top
Lavington
ALBURY
Wodonga
Hume Reservoir
Howlong
COROWA
Rutherglen
Mulwala
YARRAWONGA
Tocumwal
Finley
Berrigan
Cobram
MURRAY RIVER
Numurkah
Batlow
Kyeamba
Westby
Cookardinia
Little Billabong
Woomargama
Mullengandra
Walwa

DRAWN BY THE NATIONAL MAPPING OFFICE, DEPARTMENT OF THE INTERIOR, CANBERRA, A.C.T., 1952

(e) *Relationships between Vegetation and Soil*

Changes in the native vegetation, and especially changes in the species of *Eucalyptus*, are frequently associated with changes in the soil. This was noted by Sturt (1834) and was stressed by Cambage (1925) in his plea for a botanical and soil survey of New South Wales. Beadle (1948) states that, with a few exceptions "the plant Associations are not reliable indicators of the soil zone," and that "the plant Associations are delimited primarily by rainfall."

Within the region studied in the present work there is in general a clear relationship between soil and vegetation, and climate plays a major role only where rainfall or temperature approach limiting values. The influence of soil texture on availability of moisture to the plant may also be important in these latter areas. Because of this close correlation between soil and vegetation, the boundaries of the major soil groups are defined in large measure by the boundaries of the vegetation communities. The general relationship between soil and vegetation is summarized in Table 7.

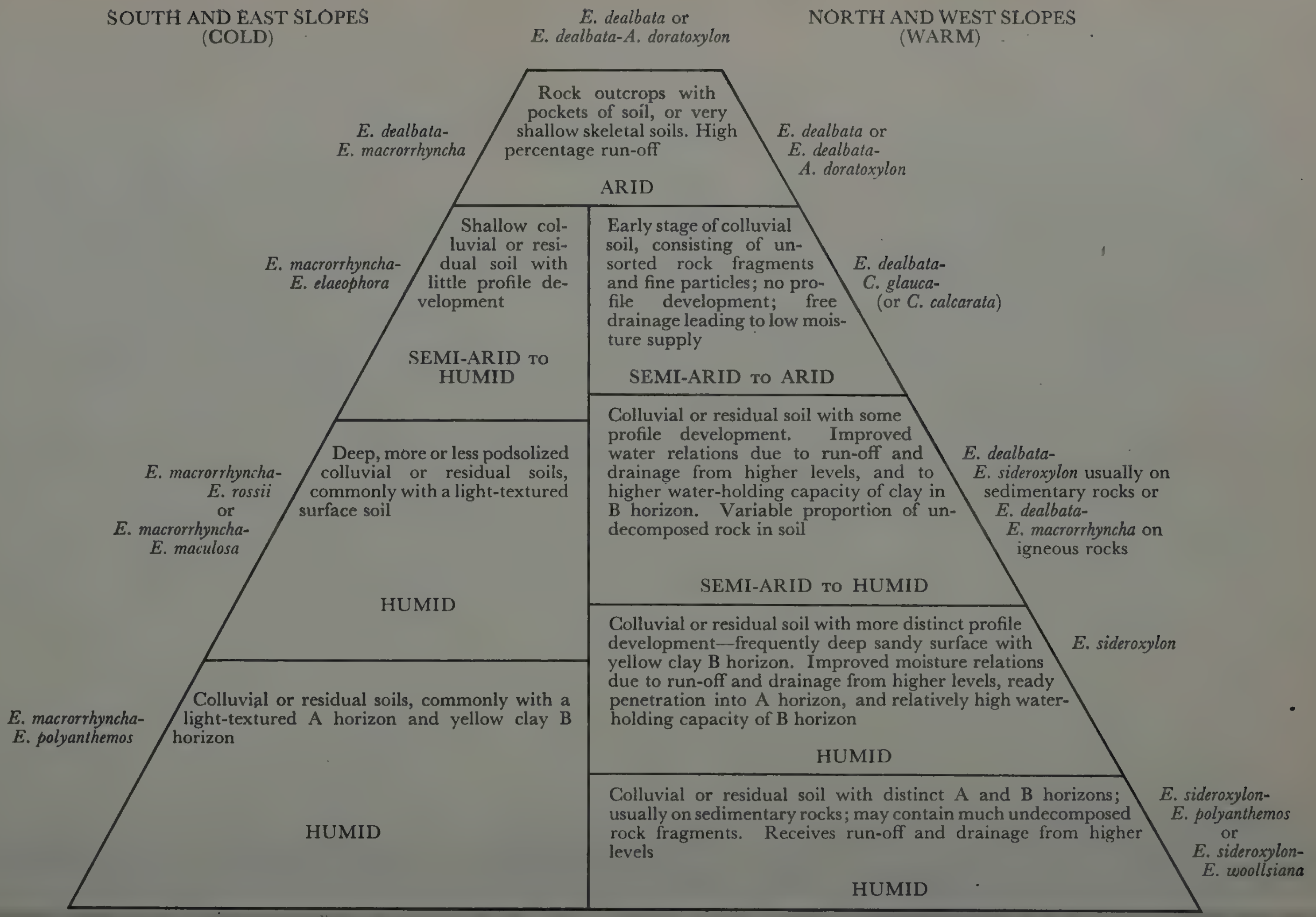
TABLE 7

GENERAL RELATIONSHIP BETWEEN SOIL AND VEGETATION

Soil Group	Alliance
Undifferentiated skeletal soils	(i) *E. dealbata-E. sideroxylon* in the warmer and drier areas (ii) *E. macrorrhyncha-E. rossii* in the cooler and wetter areas
Red and yellow podsolic soils	*E. albens*
Red-brown earths	(i) *E. woollsiana* (ii) *Acacia pendula-Atriplex nummularia* in the lower-rainfall areas especially when the A horizon is shallow
Grey and brown soils of heavy texture	*Acacia pendula-Atriplex nummularia*
Chocolate soils	*E. albens*

Perhaps the most obvious effect of soils on vegetation over a wide range of climatic conditions (too wide, in fact, for climatic factors to become limiting within or near the region) is the change from the Dry Sclerophyll Forests of the immature and skeletal soils of the low ranges to the woodland communities of the more mature podsolic soils of the eastern half and the red-brown earths of the western half of the region. The soils are commonly related to the topography, differing essentially in degree of development, and the Dry Sclerophyll Forest communities are always associated with the less mature soils.

The distribution of the various Dry Sclerophyll Forest Associations in relation to the topography and degree of development of the soil is shown in Figure 9. Towards its eastern limits the *E. dealbata-E. sideroxylon* Alliance becomes confined to the warmer aspects of the hills (north and west) and the *E. macrorrhyncha-E. rossii* Alliance occupies the cooler aspects (south and east). In Figure 9 the relationship between the plant community and its habitat is shown for both these Alliances, but it should be pointed out that the relationships shown for the former apply throughout its range within the



SOUTH AND EAST SLOPES
(COLD)

E. dealbata or
E. dealbata-A. doratoxylon

NORTH AND WEST SLOPES
(WARM)

E. dealbata-
E. macrorrhyncha

Rock outcrops with pockets of soil, or very shallow skeletal soils. High percentage run-off

ARID

E. dealbata or
E. dealbata-
A. doratoxylon

E. macrorrhyncha-
E. elaeophora

Shallow colluvial or residual soil with little profile development

SEMI-ARID TO HUMID

Early stage of colluvial soil, consisting of unsorted rock fragments and fine particles; no profile development; free drainage leading to low moisture supply

SEMI-ARID TO ARID

E. dealbata-
C. glauca-
(or *C. calcarata*)

E. macrorrhyncha-
E. rossii
or
E. macrorrhyncha-
E. maculosa

Deep, more or less podsolized colluvial or residual soils, commonly with a light-textured surface soil

HUMID

Colluvial or residual soil with some profile development. Improved water relations due to run-off and drainage from higher levels, and to higher water-holding capacity of clay in B horizon. Variable proportion of undecomposed rock in soil

SEMI-ARID TO HUMID

E. dealbata-
E. sideroxylon usually on sedimentary rocks or
E. dealbata-
E. macrorrhyncha on igneous rocks

Colluvial or residual soil with more distinct profile development—frequently deep sandy surface with yellow clay B horizon. Improved moisture relations due to run-off and drainage from higher levels, ready penetration into A horizon, and relatively high water-holding capacity of B horizon

HUMID

E. sideroxylon

E. macrorrhyncha-
E. polyanthemos

Colluvial or residual soils, commonly with a light-textured A horizon and yellow clay B horizon

HUMID

Colluvial or residual soil with distinct A and B horizons; usually on sedimentary rocks; may contain much undecomposed rock fragments. Receives run-off and drainage from higher levels

HUMID

E. sideroxylon-
E. polyanthemos
or
E. sideroxylon-
E. woollsiana

region. Except towards the eastern boundary, the *E. dealbata-E. sideroxylon* Alliance occurs on all aspects of the ranges.

On the more rocky sites of the warmer aspects with only very shallow and undeveloped soils, either the *E. dealbata* or the *E. dealbata-Acacia doratoxylon* Association occurs. The soils in these situations are subject to severe erosion during heavy falls of rain, and there is little or no opportunity for the accumulation and development of soil. Also, since the slope is commonly steep, fragments of rock fall to lower levels where they accumulate and give rise to colluvial soils on which different communities develop, according to the stage of development of the soil. There is little soil to hold moisture, and since the soil is shallow where it does occur, the habitat of these two associations has been described as arid (Fig. 9). Long periods of low moisture supply and high temperatures during the summer are inevitable, and only plants capable of withstanding dry conditions, and having a root system capable of penetrating the rock crevices, can survive.

The *E. dealbata-Callitris glauca* Association develops on the upper layers of colluvial soil, which usually consists of unsorted, more or less decomposed rock fragments of all sizes, with the coarser particles predominating. Since there is little or no development of the silt and clay fractions, drainage is free, and the water-holding capacity of the soil is low. However, the greater depth of soil enables easier root development. These areas receive the run-off from higher levels, giving a slight improvement in water relations.

At still lower levels either the *E. dealbata-E. macrorrhyncha* or the *E. dealbata-E. sideroxylon* Association develops, the former being more frequent on granitic soils and in the cooler situations while the latter is more frequent on soils derived from sedimentary rocks and in the warmer situations. Since erosive forces (especially water) are less than at higher levels, the soil has greater stability and there has been a definite movement of clay from the surface to the illuvial horizons. This habitat receives additional water as run-off and drainage from higher levels and the water-holding capacity of the B horizon is relatively high. It has been described as semi-arid to humid (Fig. 9). The slope here is frequently fairly steep and the surface soil (commonly deep) is usually sandy, so that this habitat cannot always be regarded as humid and is commonly subjected to severe desiccation during the summer.

Where run-off and drainage are less than in any of the preceding sites, and where soil formation has proceeded to a further stage, the *E. sideroxylon* Association is found. The slope is usually gentle and the soil has a deep, sandy A horizon and a light to medium clay B horizon. In these areas additional water is usually received in the form of run-off from higher levels. These areas are classed as humid (Fig. 9) because penetration of water into the surface soil is not impeded, and the water-holding capacity of the subsoil is relatively high.

Fig. 9.—General relation between aspect, topography, and soil on the distribution of the Dry Sclerophyll Forest communities in the eastern portion of the region. The right-hand half of the diagram also shows the general relation between topography and soil and the distribution of the associations within the *Eucalyptus dealbata-E. sideroxylon* Alliance throughout the region. One or more of the associations may be missing in any particular locality.

Towards the bottom of the slopes and adjoining the woodland communities of the mature soils, either the *E. sideroxylon-E. woollsiana* Association or the *E. sideroxylon-E. polyanthemos* Association is found. The former occurs where the immature soils grade into the red-brown earths carrying *E. woollsiana*, and the latter where they grade into the podsolics carrying *E. albens*. These soils have developed distinct A and B horizons, but may contain a high proportion of undecomposed rock fragments.

On the cooler aspects towards the eastern boundary similar relationships between soil, topography, and vegetation have been observed. Where rock outcrops occur towards the tops of the hills, giving in effect a cool but arid environment, the *E. dealbata-E. macrorrhyncha* Association may occur. These communities in general do not appear more than a short distance from the top of the slope. At somewhat lower levels, where definite though relatively little soil development has occurred and where moisture relations are somewhat better, *E. macrorrhyncha-E. elaeophora* Association is found. At still lower levels on more mature and deeper soils, either the *E. macrorrhyncha-E. rossii* or the *E. macrorrhyncha-E. maculosa* Association appears, while at the lowest level on soils which may be quite well-developed podsolics, and bordering on the woodland communities (usually *E. albens* Association), *E. macrorrhyncha-E. polyanthemos* Association is found.

The boundaries between the *E. albens* Alliance and the *E. woollsiana* Alliance are always associated with a major soil change. *E. albens* communities invariably appear on the podsolic soils, while *E. woollsiana* communities are found on the red-brown earths, or, in the eastern limits of the range of these communities, on interzonal soils which more closely resemble red-brown earths than podsolics. In fact, the boundary between these two major soil groups is defined with considerable accuracy by the boundary between the *E. albens* and the *E. woollsiana* Alliances.

E. albens communities are found on a wide range of soils developed from a wide range of parent materials, including granites, basalt, sedimentary rocks of various kinds, and metamorphic rocks (derived from both igneous and sedimentary rocks).

The distribution of the various associations within the *E. albens* Alliance is related to the topography, stage of development of the soil, and moisture supply. Towards the tops of the hills, where the soils may be shallow with rock outcrops and where there is a high proportion of run-off, rather stunted *E. albens* communities occur. *Brachychiton populneus* is a common species in such situations, and *Casuarina stricta* may be prominent. In similar topographic situations in the higher-rainfall areas the *E. albens-E. macrorrhyncha* Association occurs.

On the deeper soils of the slopes of the hills, well-developed stands of *E. albens* Tall Woodland are found, and in these communities *E. melliodora* and *E. blakelyi* frequently occur, but do not reach the status of dominants. There is a gradual change in dominance down the slope, until on the deeper, more highly leached colluvial and alluvial soils at the lower levels the *E. albens-E. melliodora-E. blakelyi* Association makes its appearance, with *E. stuartiana* commonly occurring in the wetter areas. On deep, sandy soils *E. melliodora* and *E. blakelyi* are codominant to much higher levels than on soils of heavier texture.

The *E. albens-Callitris glauca* Association has been observed only on sandy soils towards the western limits of the Alliance.

The *E. woollsiana* Alliance occurs on the red-brown earths, and in areas with a mean annual rainfall of 18 in. or more it is found on all types of soil within this major soil group. The occurrence of the various associations is clearly related to soil texture.

On loams or heavier-textured soils the *E. woollsiana* Association is found, with little or no *Callitris glauca.* On the lighter-textured soils (sandy loams to sands) *C. glauca* becomes a dominant member of the community, giving the *E. woollsiana-C. glauca* Association. On light-textured soils with a deep A horizon *E. melliodora* is frequently codominant with *C. glauca,* giving the *E. melliodora-C. glauca* Association. *E. blakelyi* does not occur frequently in this alliance, but is found most commonly on the deep, sandy soils associated with *E. melliodora* and *C. glauca.* *E. melliodora* is also found on light to medium-textured soils with good drainage in situations receiving an augmented water supply as run-off from surrounding areas. On the residual soils, where the topography is usually rolling to hilly, there is little change in the vegetation between the top and bottom of the hills. *Brachychiton populneus* may occur on the more shallow soils towards the tops of the hills.

As rainfall becomes limiting the *E. woollsiana* Alliance becomes confined more and more to the lighter-textured soils, especially those with a deep A horizon, until finally it is found at its western limits only on deep sands. The effect of soil texture with decreasing rainfall first becomes pronounced to the north-east of Urana (rainfall < 18 in.); where *Acacia pendula* replaces *E. woollsiana* on the alluvial red-brown earths with shallow surface horizons, or where the surface soil has a slightly heavier texture (loams or heavier). *A. pendula,* however, is always found on alluvial soils and does not occur on the residuals.

In the area between Darlington Point and Jerilderie, the *E. woollsiana* Alliance is confined to soils with a deep, light-textured A horizon, while the more typical red-brown earths of this area, with a shallow surface soil, are occupied by *Acacia pendula.*

It is apparent, therefore, that the limits of distribution of the *E. woollsiana* Alliance are determined by both climate and soil, the influence of the latter being seen either when there is a change from one major soil group to another, or when one of the climatic factors is approaching a limiting value. It would appear that the dominating climatic factor limiting *E. woollsiana* communities to the lighter-textured soils in the lower-rainfall areas is moisture. Water penetration in these soils is not inhibited and there is little or no run-off. Further, absorption of water by the plant from sandy soils is more readily accomplished than from soils with a high percentage of clay, which holds the water with much greater force. The result is that water relations, both supply and removal, are adequate even though total precipitation is low.

Similar relationships can be shown for the distribution of *Acacia pendula.* This species occurs prominently on the red-brown earths of loam to heavy texture or those with a shallow sandy loam surface (less than 3 in.) chiefly on the plains to the north and west of Urana. Smaller areas occur elsewhere, as indicated previously (see also vegetation map). However, as one proceeds westwards to areas of lower rainfall, *A. pendula* tends to become more and more prominent on the grey and brown soils of heavy texture. These are heavy clays and clay loams which are usually at slightly lower levels than the red-brown earths, and receive run-off from the higher surrounding country. They are the best-watered areas but have relatively poor drainage, and provide the most suitable sites for *A. pendula* where rainfall is limiting. This species grows on these heavy-textured soils in the eastern portion of the plains, but not so commonly as on the red-brown earths. The natural dominant on the grey and brown soils of heavy texture in the higher-rainfall districts appears to have been *Atriplex nummularia* with scattered trees of *A. pendula.*

Though the occurrence of *A. pendula* as a dominant on the red-brown earths and grey and brown soils of heavy texture can, in general, be explained on the basis of a combined climate-soil effect, this is not so for the Bullenbung Plain, between Wagga and Lockhart, where the rainfall is about 20 in. Proceeding westwards from Mundowie one passes through typical *E. woollsiana* and *E. woollsiana-C. glauca* Associations, depending on the soil, until there is a sudden change to a disclimax grassland on the Bullenbung Plain, where the soils are predominantly heavy clays or clay loams belonging to the grey and brown soils of heavy texture. It would appear that *Acacia pendula* was once dominant on this plain and that *Atriplex nummularia* may have been the dominant in the shrub stratum since the soils appear to be essentially the same as those of typical areas further west; the disclimax communities are dominated by *Stipa aristiglumis* as are those to the west, and the subordinate flora is similar. However, no relict areas occur here, and no definite confirmatory evidence has been found regarding the occurrence of *A. nummularia.*

On passing out of the Bullenbung Plain on its western boundary, there is first a mixed community of *E. woollsiana* and *A. pendula* followed by typical *E. woollsiana-C. glauca* on light-textured soils of the red-brown earths.

The fact that there is a general relationship between soil and vegetation should not be taken as evidence that the current vegetation *per se* has played a significant role in the formation of the soil. Robinson (1935) states, "Vegetation cannot be accorded the rank of an independent variable, since it is itself closely governed by situation, soil, and climate. And, therefore, whilst the intimate relation between natural vegetation and soil cannot be overlooked, it must be regarded mainly as a reciprocal contract." Jenny (1941) points out the difficulties involved in determining "the vegetational component of the biotic factor" since the vegetation found growing on any area will change with changes in climate, soil, and topography. At the same time he stresses the important effects of vegetation on a soil, whether or not it is to be regarded as a soil-forming factor.

In Australia, various species of the genus *Eucalyptus* are found more or less confined to certain soils which show major differences in their important characteristics. It would be difficult, if not impossible, to demonstrate differences in the composition of the litter of any two species of *Eucalyptus*, sufficient to play an important part in the development of two major soil groups. Perhaps the most clear-cut example from the present study is the growth of *E. albens* on the red and yellow podsolic soils, and *E. woollsiana* on the red-brown earths. These two species are very closely related; and yet they are, with few exceptions, confined to the podsolic soils and red-brown earths respectively. Evidence from the present study therefore supports the theory that the soil governs the kind of plants which will grow on it, and that the subsequent influence of the vegetation on the soil is secondary.

(*f*) *Life-form Spectra*

The life-form spectra have been calculated for each alliance and for the whole region on the list of endemic species only. These spectra are shown in Table 8, which also shows Raunkiaer's "normal" spectrum (Raunkiaer 1934). Since the life-form spectrum is based on the species list of a community or region, the values depend to a large extent on the number of stands examined. The figures given in Table 8 for the *Eucalyptus camaldulensis, E. macrorrhyncha-E. rossii,* and *E. largiflorens* Alliances are based on a few stands only, and are subject to considerable modification when a larger number of stands is included. Even so, the spectra given for these communities agree well with those of the other communities and of the whole region.

TABLE 8

LIFE-FORM SPECTRUM FOR EACH ALLIANCE AND FOR THE WHOLE REGION

Source	No. of Species	MM	M	N	Ch	H	G	Th
E. dealbata-E. sideroxylon Alliance	139	6·5	11·5	29·5	14	19	6·5	13
E. macrorrhyncha-E. rossii Alliance	61	7	13	16	16	33	5	10
E. camaldulensis Alliance	29	3·5	3·5	—	14	41·5	3	34·5
E. woollsiana Alliance	203	4	9	11	15	34	6	21
E. albens Alliance	122	5	11	4	12	40	8	20
E. largiflorens Alliance	38	—	5	7·5	15·5	42	—	30
Acacia pendula-Atriplex nummularia Alliance	134	—	0·5	4	21	34	7·5	33
Whole region	333	5	10	18	14	28	5	20
"Normal" spectrum*	1000	8	18	15	9	26	4	13

*Omitting stem succulents, epiphytes, and hydrophytes.

Allan (1937) has referred to the difficulties of applying Raunkiaer's system in the Southern Hemisphere, and stresses the difficulty of distinguishing satisfactorily between the chamaephytes and the hemicryptophytes. In determining the life forms of the plants of the south-eastern Riverina the same difficulties were encountered.

The life-form spectrum for the region shows a preponderance of hemicryptophytes and therophytes, but neither of these values is high enough to bring the region as a whole within Raunkiaer's hemicryptophyte or therophyte climates. With the except of the *E. dealbata-E. sideroxylon* Alliance, which is strongly nanophanerophytic, all the communities contain a high proportion of hemicryptophytes, and (except the *E. macrorrhyncha-E. rossii* Alliance) a relatively high proportion of therophytes. These communities therefore most closely approximate the hemicryptophyte climate as defined by Raunkiaer (1934), which he states is characteristic of the cold temperate zone.

The distribution of the *E. dealbata-E. sideroxylon* Alliance within the region is determined by edaphic and not by climatic conditions. The strong nanophanerophytic element in this community and the weak hemicryptophytic element as compared with the other alliances appear therefore to be an expression of edaphic conditions rather than climatic conditions.

V. ACKNOWLEDGMENTS

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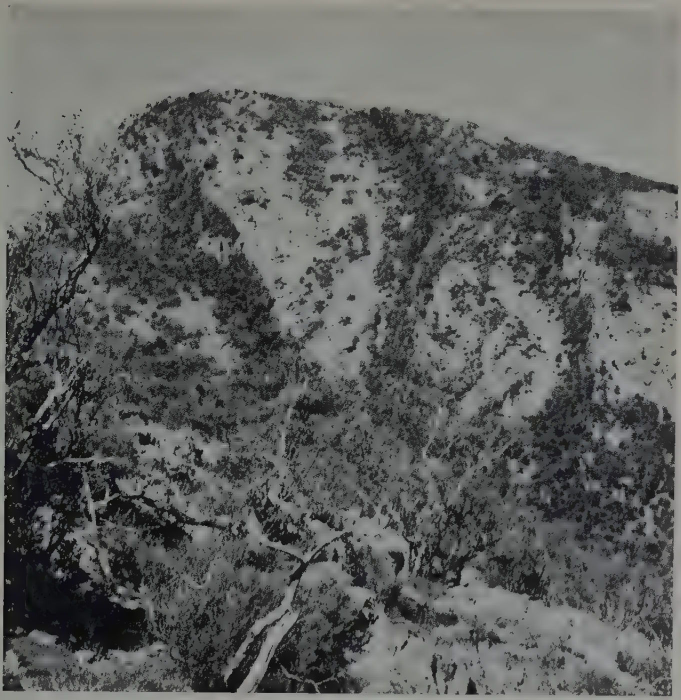

Fig. 1.—*Eucalyptus dealbata-Acacia doratoxylon* Association on the upper north-west slopes of The Rock.

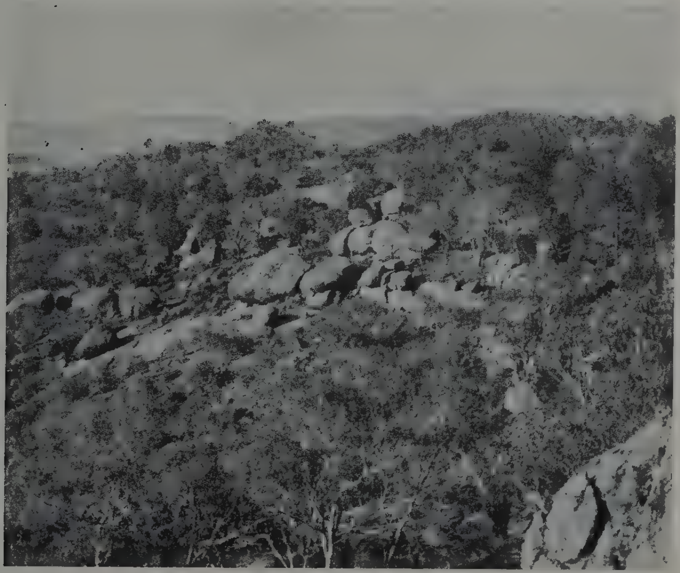

Fig. 2.—*Eucalyptus dealbata-Acacia doratoxylon* Association with some *Callitris glauca* on granite range near Cootamundra. In the distance is *E. albens* woodland.

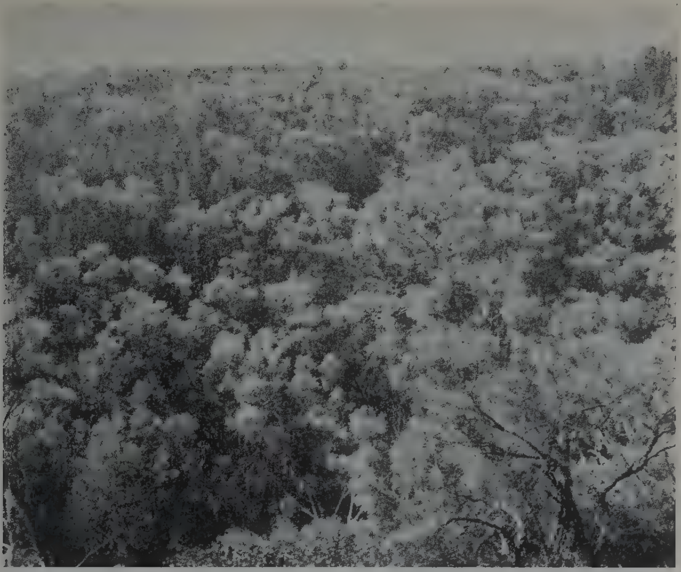

Fig. 1.—*Eucalyptus dealbata, Acacia doratoxylon,* and *Callitris calcarata* on steep, rocky slopes of the western aspect of Yambla Range.

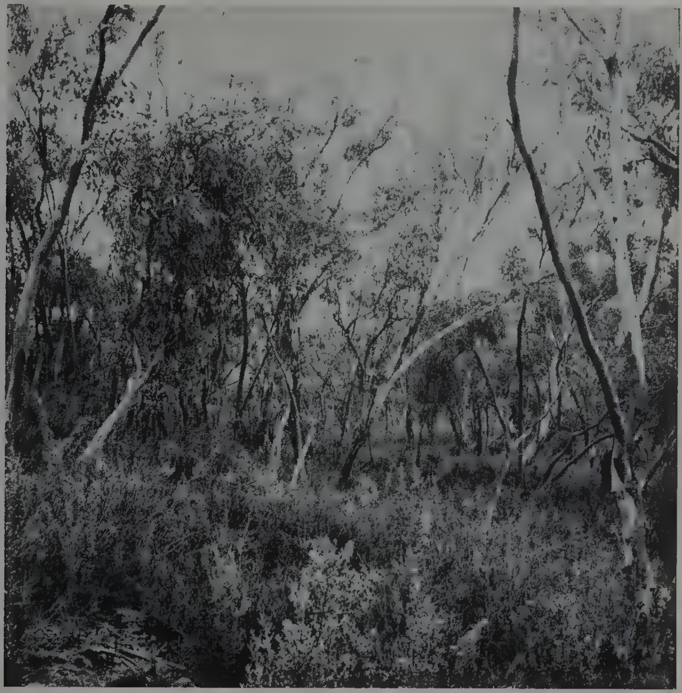

Fig. 2.—*Eucalyptus dealbata* Association with shrub stratum of *Hibbertia linearis* and *Stypandra glauca* on granite between Wagga and Mangoplah.

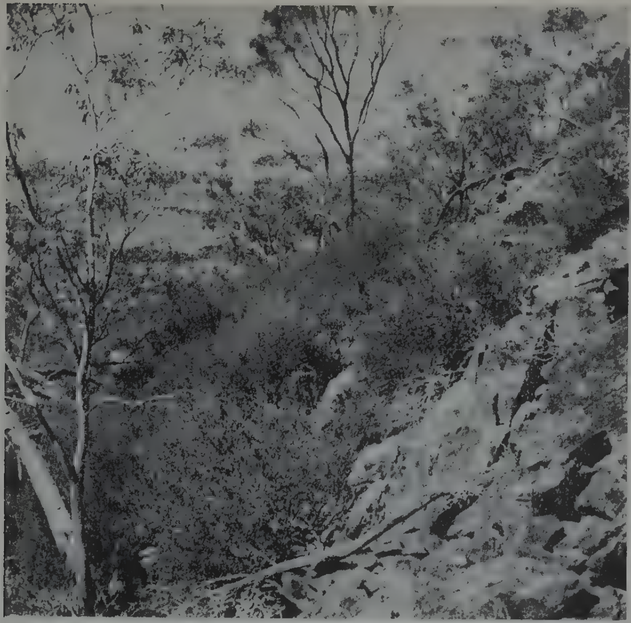

Fig. 1.—*Eucalyptus dealbata-Acacia doratoxylon* Association on The Rock. The dominant member of the shrub stratum is *Dodonaea viscosa*.

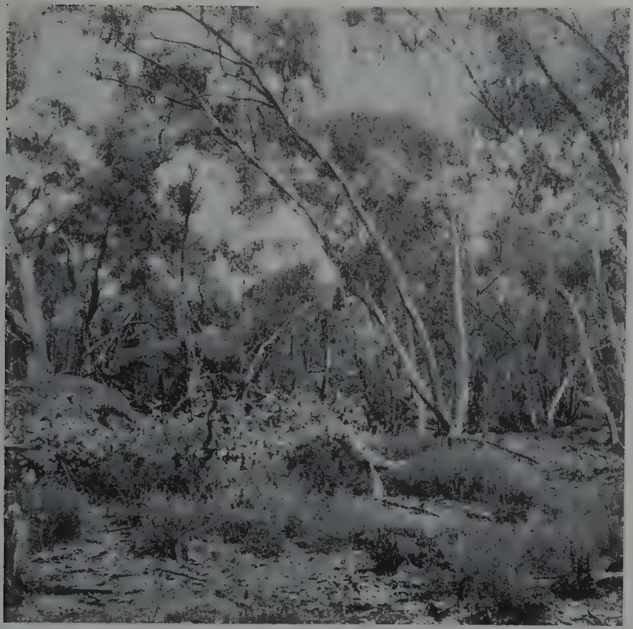

Fig. 2.—*Eucalyptus dealbata-Acacia doratoxylon* Association on granite, near Chiltern, Vic.

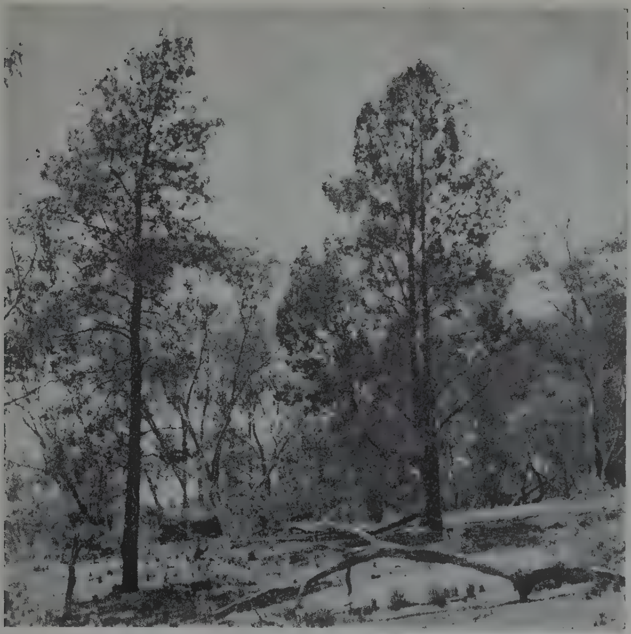

Fig. 1.—*Eucalyptus dealbata-Callitris glauca* Association with sparse shrub stratum (chiefly *Hibbertia linearis*) between Wagga and Mangoplah.

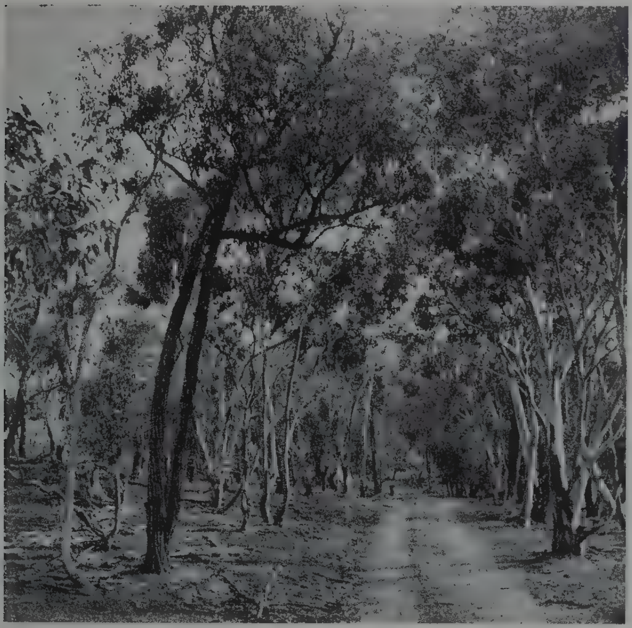

Fig. 2.—*Eucalyptus dealbata-E. macrorrhyncha Association* between Pulletop and Gregadoo.

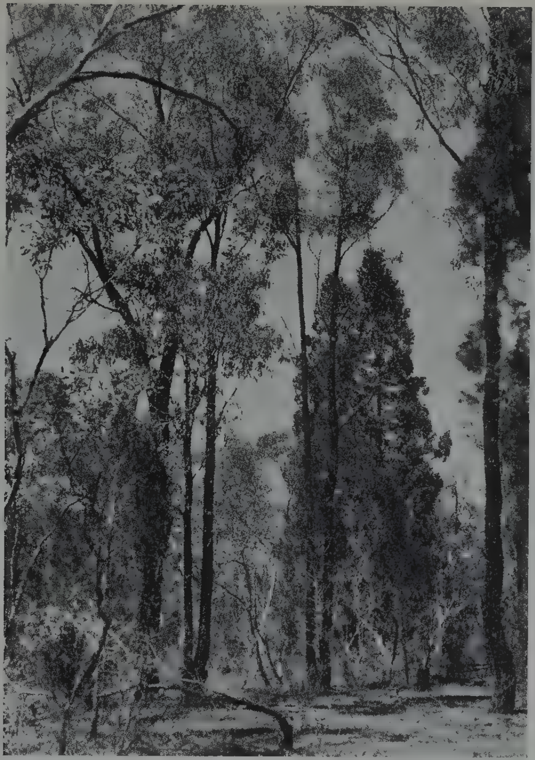

Fig. 1.—*Eucalyptus dealbata-E. sideroxylon* Association with *Callitris glauca* between Temora and Ariah Park.

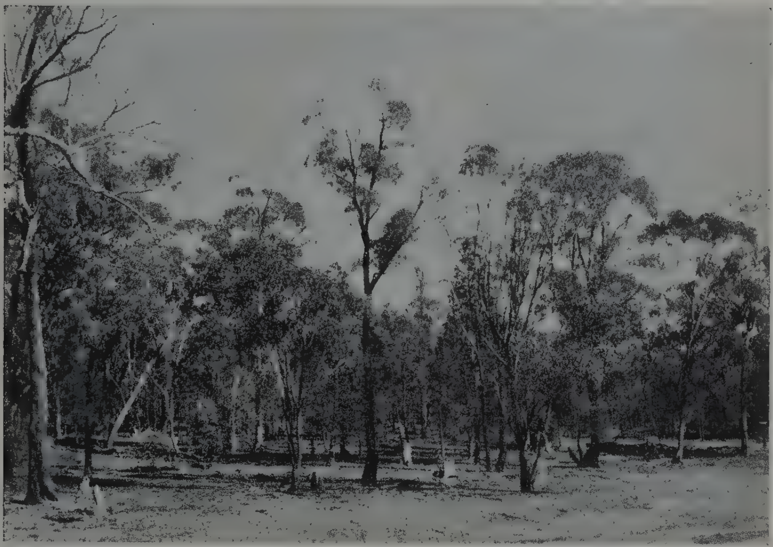

Fig. 2.—*Eucalyptus sideroxylon-E. woollsiana* Association between Temora and Cootamundra.

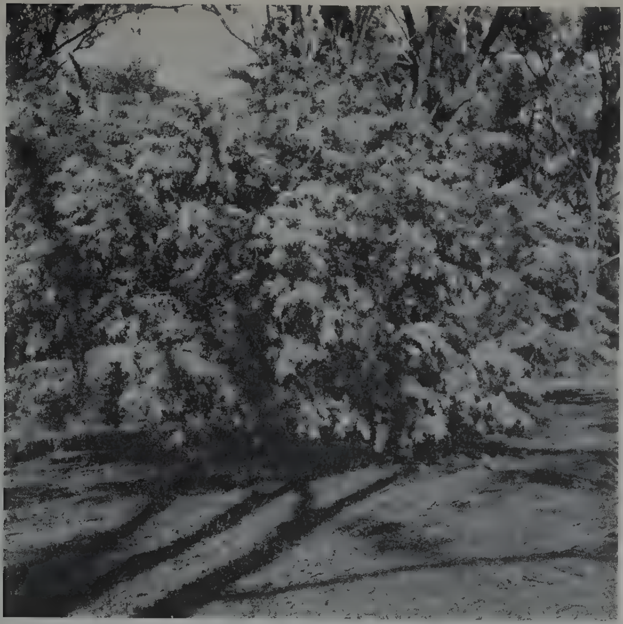

Fig. 1.—*Acacia baileyana* in *Eucalyptus sideroxylon-E. woollsiana* Association near Stockinbingal.

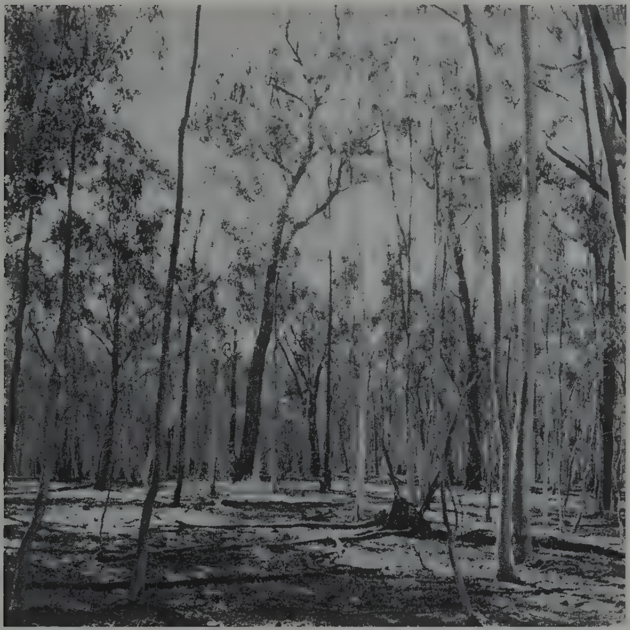

Fig. 2.—*Eucalyptus macrorrhyncha-E. rossii* Association on deep sand between Morven and Mangoplah. Note the absence of shrubs in this community.

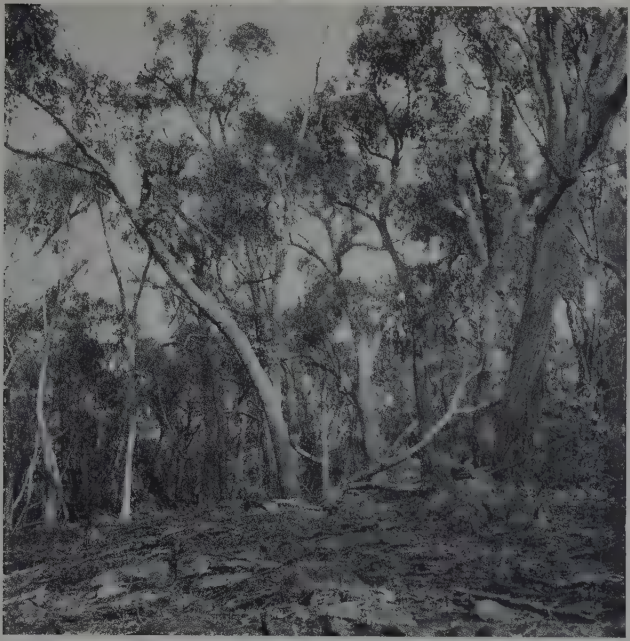

Fig. 1.—*Eucalyptus macrorrhyncha-E. elaeophora* Association on Yambla Range.

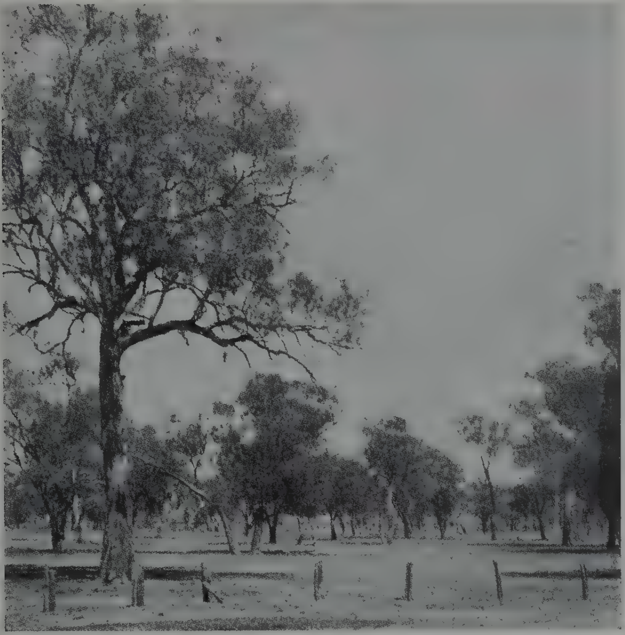

Fig. 2.—*Eucalyptus woollsiana* Association at Daysdale.

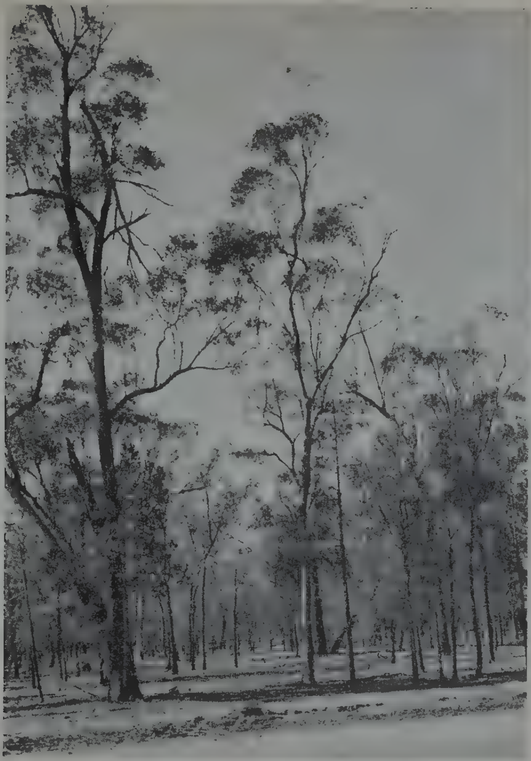

Fig. 1.—*Eucalyptus woollsiana-Callitris glauca* Association between Ardlethan and Coolamon.

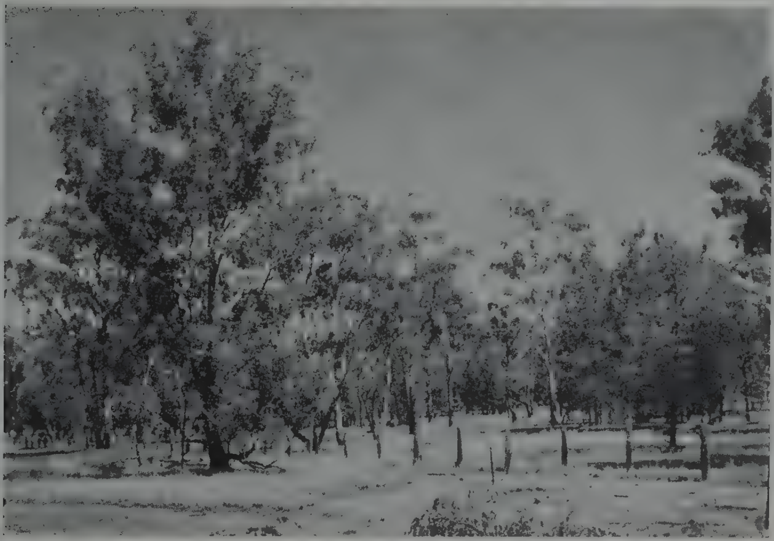

Fig. 2.—*Eucalyptus melliodora-Callitris glauca* Association on deep sand between Boree Creek and Urana.

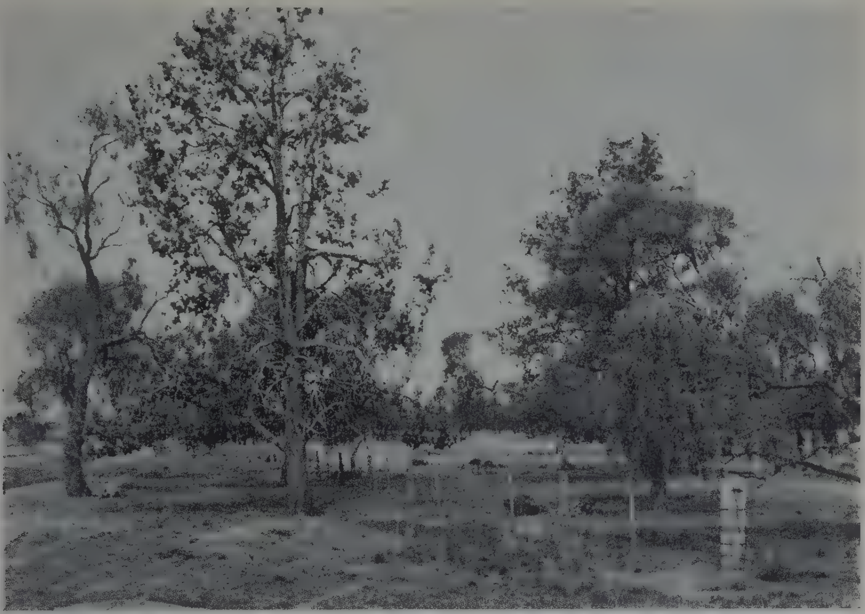

Fig. 1.—Partially cleared sandhill between Urana and Jerilderie with *Callitris glauca, Acacia salicina,* and *Hakea leucoptera.*

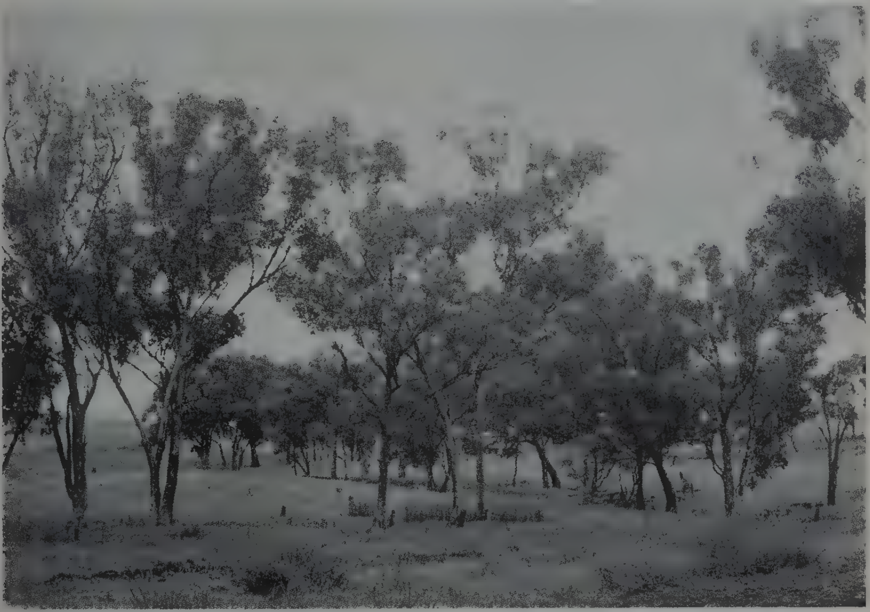

Fig. 2.—*Eucalyptus albens* Association (partially cleared) between Ladysmith and Coreinbob.

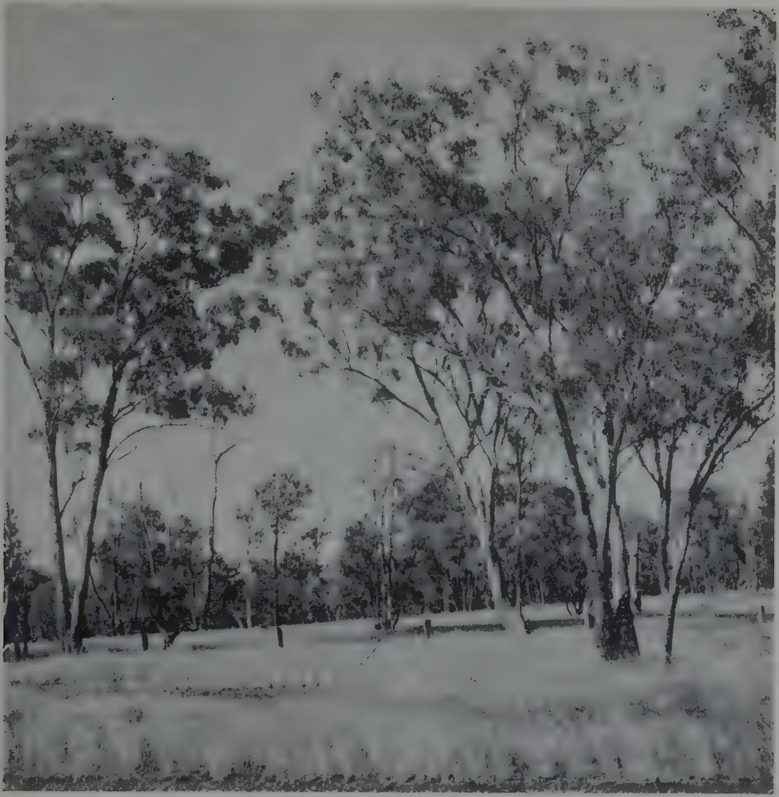

Fig. 1.—*Eucalyptus albens-Callitris glauca* Association (partially cleared) on sandy soil between Wagga and Coolamon. The dominant species in the herbaceous stratum is *Stipa falcata*.

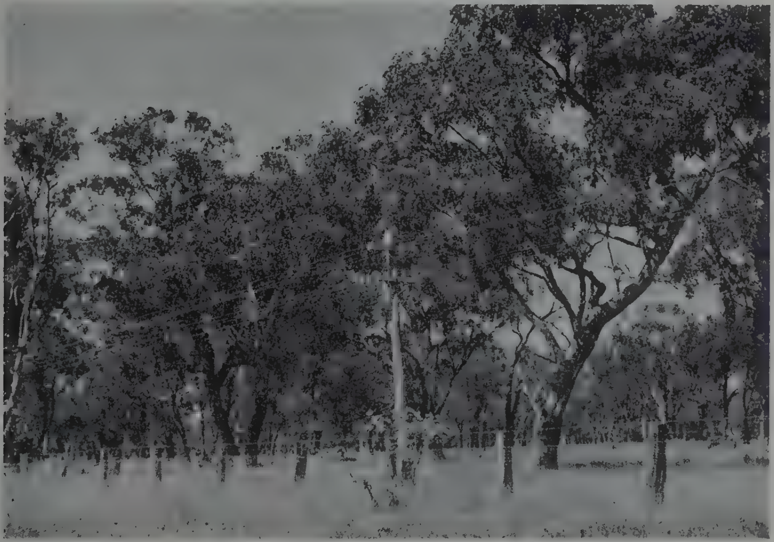

Fig. 2.—*Eucalyptus albens-E. melliodora-E. blakelyi* Association between Wagga and Kyeamba.

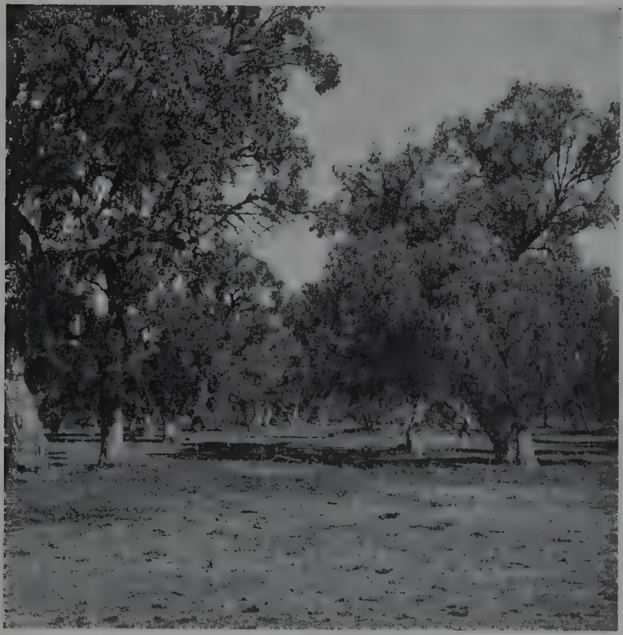

Fig. 1.—*Eucalyptus largiflorens* Association near Jerilderie.

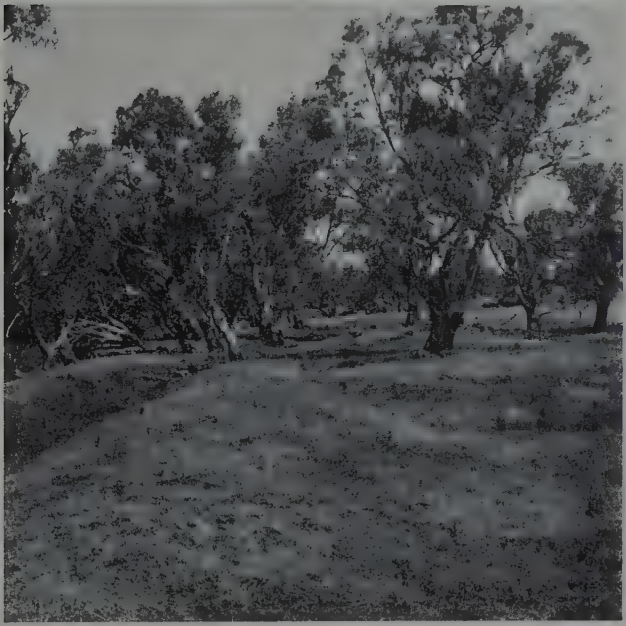

Fig. 2.—*Eucalyptus camaldulensis* (savannah woodland) Association on the Murray River Flats at Howlong.

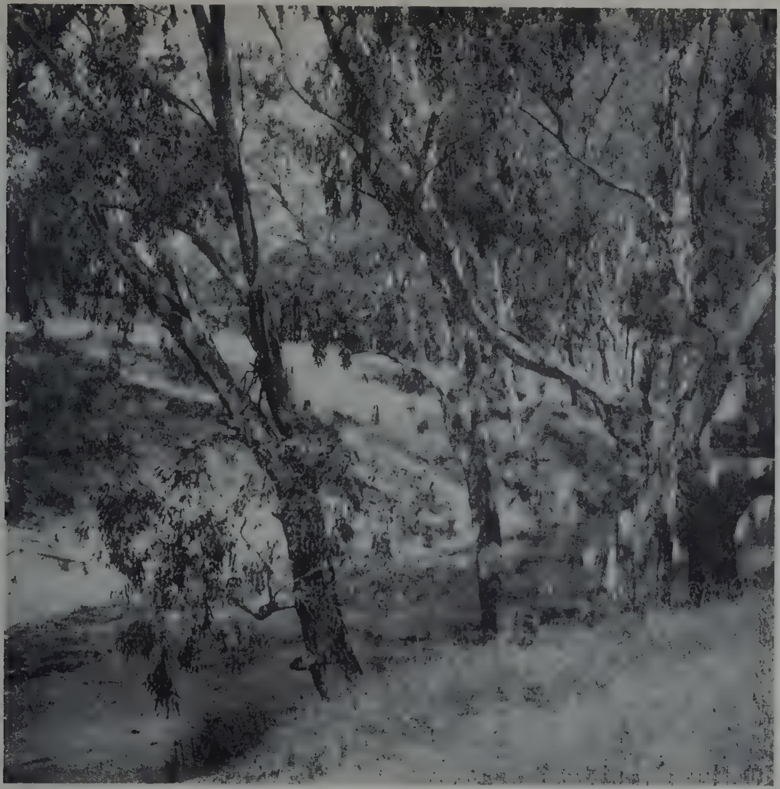

Fig. 1.—*Eucalyptus camaldulensis* on banks of Billabong Creek.

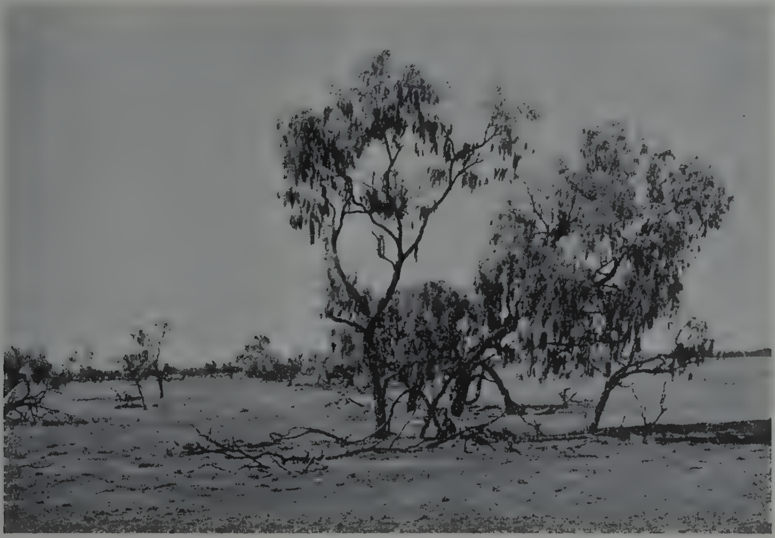

Fig. 2.—Partially cleared *Acacia pendula* on red-brown earth about 20 miles south of Darlington Point.

VEGETATION OF SOUTH-EASTERN RIVERINA, N.S.W. I

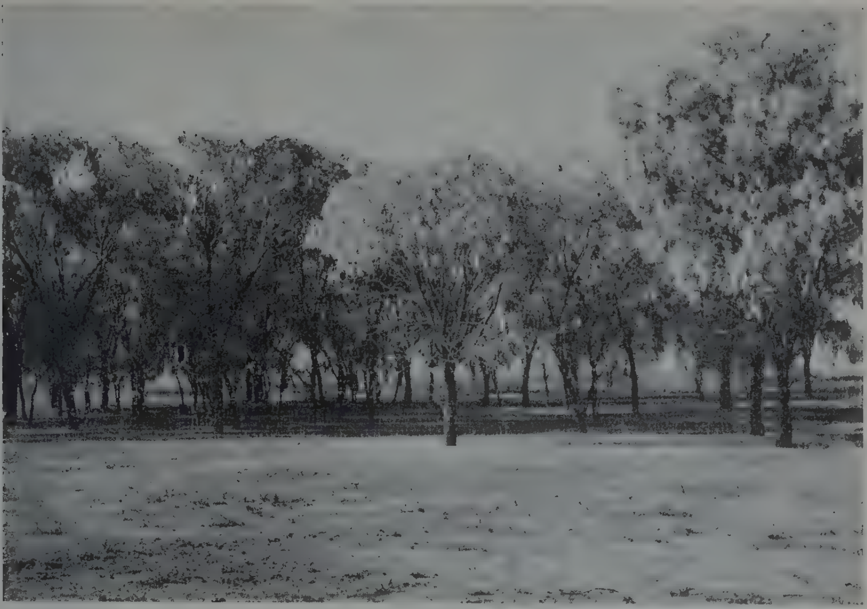

Fig. 1.—Young stand of *Acacia pendula* in a protected area near Jerilderie.

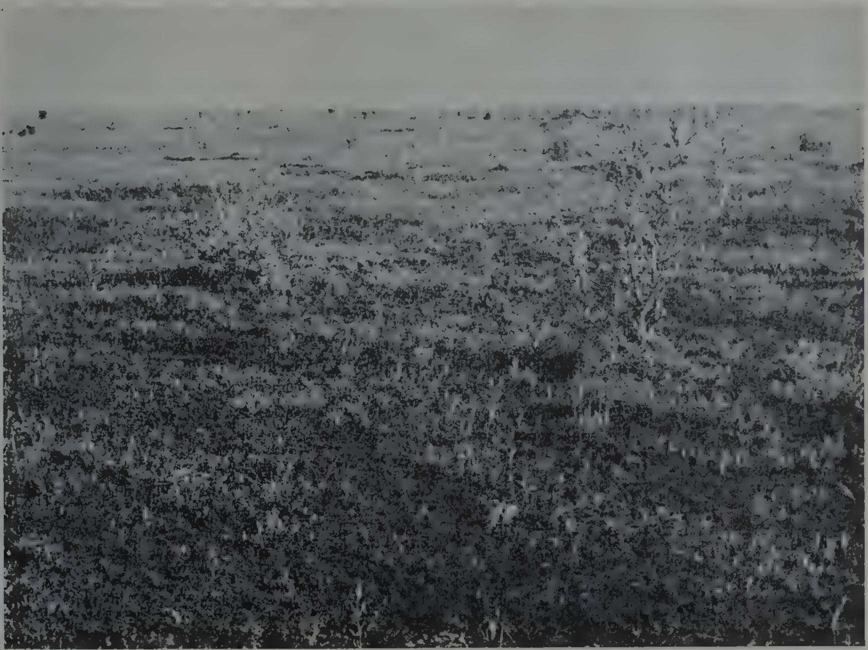

Fig. 2.—Early stage in regeneration of *Acacia pendula* near Jerilderie.

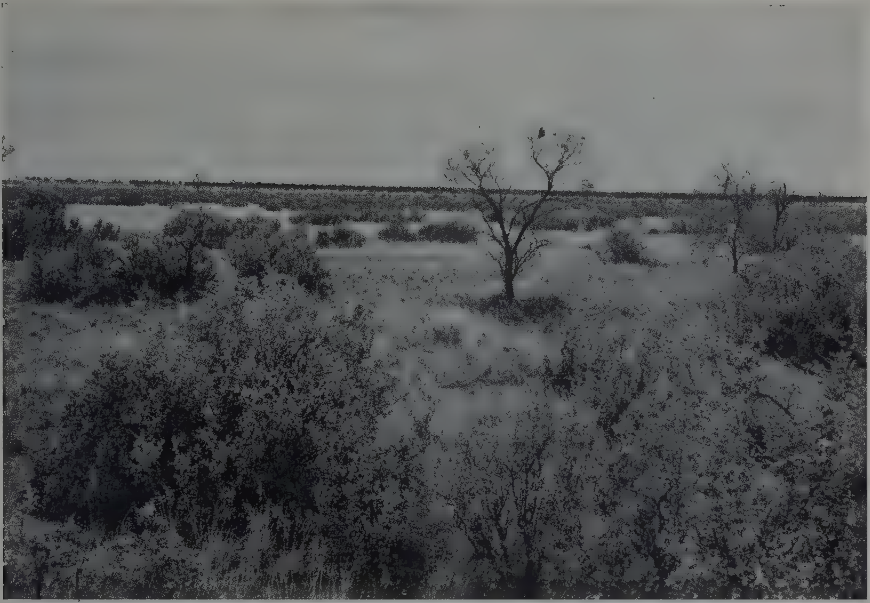

Fig. 1.—A vigorous stand of *Atriplex nummularia* with *Acacia pendula* at "Coonong", near Urana.

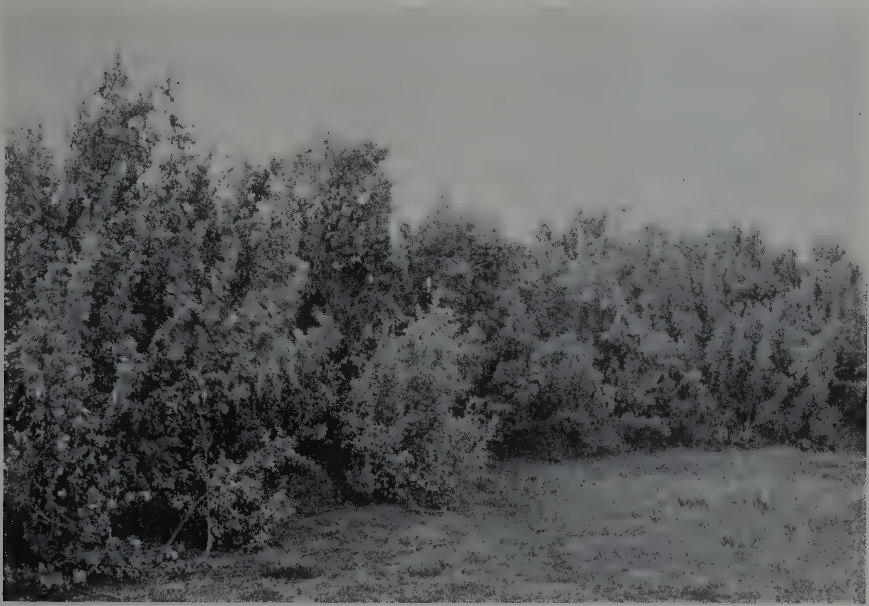

Fig. 2.—*Atriplex nummularia* at "Coonong," near Urana. These bushes were at least 10 ft high when photographed, and occur in the same stand as shown in Figure 1.

VEGETATION OF SOUTH-EASTERN RIVERINA, N.S.W. I

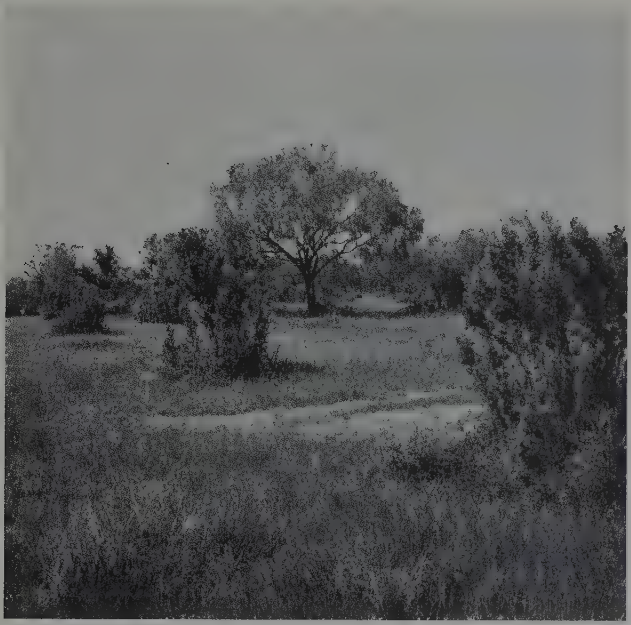

Fig. 1.—*Acacia pendula* and *Atriplex nummularia* at "Coree", near Jerilderie.

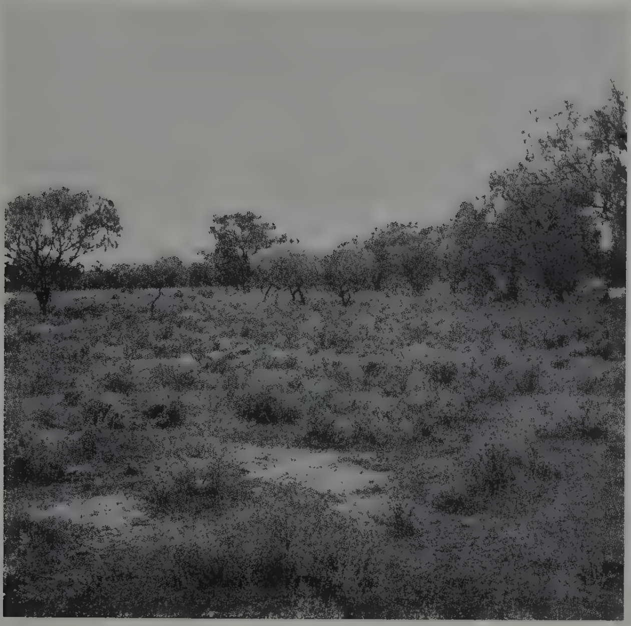

Fig. 2.—*Eucalyptus largiflorens, Acacia pendula,* and *Atriplex vesicaria* at "Coree", near Jerilderie.

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APPENDIX I

SPECIES OCCURRING IN EACH ALLIANCE, TOGETHER WITH THE LIFE FORM (RAUNKIAER 1934) OF EACH SPECIES

MM = megaphanerophyte and mesophanerophyte; M = microphanerophyte; N = nanophanerophyte; Ch = chamaephyte; H = hemicryptophyte; G = geophyte; Th = therophyte. × Indicates presence of the species; * exotic species

Species	Life Form	Alliance						
		E. dealbata- *E. sideroxylon*	*E. macrorhyncha-* *E. rossii*	*E. camaldulensis*	*E. woollsiana*	*E. albens*	*E. largiflorens*	*Acacia pendula-* *Atriplex nummularia*
POLYPODIACEAE								
Cheilanthes tenuifolia Swartz	G	×	×		×	×		×
OPHIOGLOSSACEAE								
Ophioglossum coriaceum A. Cunn.	G			×	×	×		
MARSILIACEAE								
Marsilia drummondii A. Br.	H				×		×	×
PINACEAE								
Callitris calcarata R. Br.	M-MM	×						
C. glauca R. Br.	M-MM	×	×		×	×		
GRAMINEAE								
Agropyron scabrum (R. Br.) Beauv.	H	×	×	×	×	×		
Agrostis avenacea Gmel.	Th					×		×
**Aira caryophyllea* L.	Th	×	×		×	×		
Alopecurus geniculatus L.	H							×
Amphibromus neesii Steud.	H			×	×		×	×
Aristida armata Henr.	Ch	×			×			
A. behriana F. Muell.	Ch	×		×	×	×		
A. calycina R. Br.	Ch							×
A. jerichoensis var. *subspinulifera* Henr.	Ch	×			×			
A. ramosa R. Br.	Ch	×	×		×	×		
**Avena barbata* Brot.	Th				×	×		×
Bothriochloa ambigua S. T. Blake	Ch	×			×	×		
**Briza maxima* L.	Th					×		
**B. minor* L.	Th		×	×	×	×		
**Bromus carthaticus* Vahl.	Th			×	×			
**B. mollis* L.	Th	×	×	×	×	×	×	×
**B. rigidus* Roth.	Th		×	×	×	×		×
**B. rubens* L.	Th	×			×	×		×
Chloris acicularis Lindl.	H				×	×		×

Appendix I (*Continued*)

Species	Life Form	*E. dealbata*-*E. sideroxylon*	*E. macrorrhyncha*-*E. rossii*	*E. camaldulensis*	*E. woollsiana*	*E. albens*	*E. largiflorens*	*Acacia pendula*-*Atriplex nummularia*
		Alliance						
GRAMINEAE (*Continued*)								
C. truncata R. Br.	H	×	×		×	×	×	×
Cynodon dactylon (L.) Pers.	H			×	×	×		
Dactyloctenium radulans (R. Br.) Beauv.	Th				×			
Danthonia spp.	Ch	×	×	×	×	×	×	×
Danthonia pallida R. Br.	Ch	×	×					
D. simulans J. W. Vickery	Ch				×			
D. caespitosa Gaud.	Ch				×	×		
D. auriculata J. M. Black	Ch					×		
D. duttoniana A. B. Cashmore	Ch							
Danthonia aff. *linkii* var. *fulva* J. W. Vickery	Ch	×						
Dicanthium sericeum (R. Br.) A. Camus	H				×			
Digitaria ammophila (F. Muell.) Hughes	H				×			
D. brownii (R. & S.) Hughes	H	×						
D. coenicola (F. Muell.) Hughes	H				×			
D. divaricatissima (R. Br.) Hughes	H				×			
D. sanguinalis Scop.	H				×			
Enneapogon nigricans (R. Br.) Beauv.	H		×		×	×		×
Eragrostis australasica (Steud.) C. E. Hubbard	Ch							×
**E. cilianensis* (All.) Link. ex Lutati	Th				×	×		×
E. elongata (Willd.) Jacq.	H				×	×		×
E. lacunaria F. Muell.	H	×			×	×		×
E. parviflora (R. Br.) Trin.	Th	×			×	×		×
**Hordeum leporinum* Link.	Th	×	×	×	×	×	×	×
**Koeleria phleoides* Pers.	Th	×			×	×		
**Lamarckia aurea* (L.) Moench.	Th					×		×
**Lolium loliaceum* (Bory & Chaub) Hand-Mazz	Th				×			
**L. rigidum* Gaud.	Th			×	×	×		×
**L. perenne* L.	H			×				
Neurachne mitchelliana Nees	H				×	×		
Panicum decompositum R. Br.	H				×			×
P. effusum R. Br.	H	×	×		×	×	×	×
P. prolutum F. Muell.	H				×		×	×
P. whitei J. M. Black	H				×			
Paspalidium gracile (R. Br.) Hughes	H				×			
P. jubiflorum (Trin.) Hughes	H				×			
**Pennisetum villosum* R. Br.	H				×			
**Phalaris minor* Rhetz.	Th			×		×		

Appendix I (*Continued*)

Species	Life Form	Alliance						
		E. dealbata- *E. sideroxylon*	*E. macrorrhyncha-* *E. rossii*	*E. camaldulensis*	*E. woollsiana*	*E. albens*	*E. largiflorens*	*Acacia pendula-* *Atriplex nummularia*
GRAMINEAE (*Continued*)								
**Pholiurus incurvus* (L.) Schinz. & Thell	Th				×			×
**Poa annua* L.	Th			×	×			
P. australis R. Br.	H	×	×	×	×	×		
**P. bulbosa* L.	G			×	×	×		
**Psilurus incurvus* (Gonan.) Schinz. & Thell	Th	×			×	×		
**Schismus barbatus* (L.) Thell	Th				×			
Sporobolus caroli Mez.	H				×	×	×	×
Stipa aristiglumis F. Muell.	Ch			×	×	×	×	×
S. densiflora Hughes	Ch	×						
S. falcata Hughes	Ch	×	×	×	×	×	×	×
S. variabilis Nees.	Ch	×	×		×	×		×
Themeda australis (R. Br.) Stapf.	Ch	×	×		×	×		
Tragus australianus S. T. Blake	Th				×			×
Tripogon loliiformis (F. Muell.) C. E. Hubbard	Th				×	×		
**Vulpia bromoides* (L.) S. F. Gray	Th	×	×	×	×	×	×	×
CYPERACEAE								
Carex inversa R. Br.	H				×	×		
Fimbristylis dichotoma Vahl.	?H							×
JUNCACEAE								
Juncus bufonius L.	Th			×	×	×		×
J. polyanthemos Buch.	H	×	×	×	×	×	×	×
Luzula campestris (L.) DC.	H		×					
LILIACEAE								
Anguillaria dioica R. Br.	G	×			×	×		×
Arthropodium minus R. Br.	G	×			×			×
Bulbine bulbosa (R. Br.) Haw.	G				×	×		×
Dianella laevis R. Br.	H	×	×		×	×		
Dichopogon strictus J. G. Baker	G	×			×	×		×
Lomandra dura (F. Muell.) Ewart	H				×	×		
L. effusa (Lindl.) Ewart	H							×
L. leucocephala Ewart	H				×			
L. longifolia Labill.	H					×		
L. multiflora (R. Br.) J. Britten	H					×		
Lomandra spp.	H	×	×		×	×		×
Stypandra glauca R. Br.	Ch	×	×					

Appendix I (*Continued*)

Species	Life Form	Alliance						
		E. dealbata-*E. sideroxylon*	*E. macrorrhyncha*-*E. rossii*	*E. camaldulensis*	*E. woollsiana*	*E. albens*	*E. largiflorens*	*Acacia pendula*-*Atriplex nummularia*
LILIACEAE (*Continued*)								
Tricoryne elatior R. Br.	G	×			×	×		
AMARYLLIDACEAE								
Calostemma luteum Sims.	G							×
C. purpureum R. Br.	G				×			×
Hypoxis pusilla Hook. f.	G				×			×
IRIDACEAE								
**Romulea rosea* (L.) Eckl.	G				×	×		
CASUARINACEAE								
Casuarina luehmannii R. T. Baker	MM	×			×			
C. paludosa Sieb.	N	×						
C. stricta Ait.	M	×			×	×		
URTICACEAE								
**Urtica urens* L.	Th	×	×	×	×	×		
PROTEACEAE								
Grevillea floribunda R. Br.	N	×						
G. lanigera A. Cunn.	N	×						
G. parviflora R. Br.	N	×						
Hakea leucoptera R. Br.	M				×			
SANTALACEAE								
Exocarpus cupressiformis Labill.	M	×	×			×		
Fusanus acuminatus R. Br.	N	×						
LORANTHACEAE								
Loranthus miquelii Lehm.	E	×				×		
POLYGONACEAE								
Muehlenbeckia cunninghamii (Meisn.) F. Muell.	N						×	×
M. diclina (F. Muell.) J. M. Black	N						×	×
**Polygonum aviculare* L.	Th			×	×	×		×
**P. hydropiper* L.	H			×				
P. prostratum R. Br.	H			×				
**Rumex acetosella* L.	G		×			×		

Appendix I (*Continued*)

Species	Life Form	Alliance						
		E. dealbata- *E. sideroxylon*	*E. macrorrhyncha-* *E. rossii*	*E. camaldulensis*	*E. woollsiana*	*E. albens*	*E. largiflorens*	*Acacia pendula-* *Atriplex nummularia*
POLYGONACEAE (*Continued*)								
R. brownii Campd.	H	×	×	×	×	×	×	×
R. crystallinus Lange	H				×			
**R. obtusifolia* L.	H			×		×		
**R. roseus* L.	Th				×			
CHENOPODIACEAE								
Atriplex leptocarpa F. Muell.	Ch				×		×	×
A. leptocarpa F. Muell. var. *armata* Aellen	Ch				×			
A. nummularia Lindl.	N-M							×
A. pseudocampanulata Aellen	?Th							×
A. semibaccata R. Br.	Ch				×		×	×
A. spinibractea Anderson	Ch				×			×
A. vesicaria Heward ex Benth.	Ch-N							×
Bassia quinquecuspis F. Muell.	Ch				×			×
Bassia quinquecuspis F. Muell. var. *villosa* Benth.	Ch				×			
B. stelligera F. Muell.	Ch							×
B. tricuspis F. Muell.	Ch							×
B. uniflora R. Br.	Ch							×
Chenopodium atriplicinum F. Muell.	Th				×		×	×
C. carinatum R. Br.	Th	×		×	×	×		×
C. pseudomicrophyllum Aellen	Ch				×	×		×
C. triangulare R. Br.	Ch				×			
**C. vulvaria* L.	Ch							×
Enchylaena tomentosa R. Br.	Ch-N							×
Kochia aphylla R. Br.	N							×
K. ciliata F. Muell.	Ch						×	×
K. crassiloba R. H. Anderson	Ch				×	×		×
K. excavata J. M. Black	Ch							×
K. microphylla F. Muell.	N				×			
K. tamariscina (Lindl.) J. M. Black	Ch or N							×
K. tomentosa (Moq.) F. Muell.	Ch or N				×			×
K. tomentosa (Moq.) F. Muell. var. *tenuifolia* F. Muell.	Ch or N				×			×
Rhagodia nutans R. Br.	Ch				×	×		×
R. spinescens R. Br.	N or M						×	×

Appendix I (*Continued*)

Species	Life Form	Alliance						
		E. dealbata-E. sideroxylon	*E. macrorrhyncha-E. rossii*	*E. camaldulensis*	*E. woollsiana*	*E. albens*	*E. largiflorens*	*Acacia pendula-Atriplex nummularia*
CHENOPODIACEAE (*Continued*)								
**Salsola kali* L.	Th	×			×		×	×
AMARANTACEAE								
Alternanthera denticulata R. Br.	H	×		×	×	×	×	×
Trichinium macrocephalum R. Br.	H							×
T. semilanatum Lindl.	H				×	×		×
T. spathulatum R. Br.	H				×	×		×
Trichinium sp.	H	×					×	×
NYCTAGINACEAE								
Boerhaavia diffusa L.	H				×	×		×
PORTULACACEAE								
Portulaca oleracea L.	Th				×			
CARYOPHYLLACEAE								
**Arenaria serpyllifolia* L.	Th					×		
**Cerastium glomeratum* Thuill.	Th	×	×	×	×	×		
**Kohlrauschia prolifera* (L.) Kunth.	Th	×	×		×	×		
**Silene gallica* L.	Th				×	×		
Spergularia rubra (L.) J. & C. Presl.	Th				×	×	×	×
**Stellaria media* (L.) Vill.	Th			×	×	×		
RANUNCULACEAE								
**Myosurus minimus* L.	Th				×			
Ranunculus lappaceus Sm.	H or G	×			×	×		×
R. parviflorus L.	Th	×		×	×			×
PAPAVERACEAE								
**Papaver hybridum* L.	Th			×	×	×		×
CRUCIFERAE								
Alyssum linifolium Steph.	Th				×			
**Capsella bursapastoris* (L.) Moench.	Th	×		×	×	×		×
Geococcus pusillus J. Drumm.	Th				×			
Lepidium hyssopifolium Desv.	Ch or Th				×	×	×	×

Appendix I (*Continued*)

Species	Life Form	Alliance						
		E. dealbata- *E. sideroxylon*	*E. macrorrhyncha-* *E. rossii*	*E. camaldulensis*	*E. woollsiana*	*E. albens*	*E. largiflorens*	*Acacia pendula-* *Atriplex nummularia*
CRUCIFERAE (*Continued*)								
L. fasciculatum Thell.	Ch or Th				×		×	×
**Sisymbrium officinale* L.	Th				×	×		×
**S. orientale* L.	Th						×	
RESEDACEAE								
**Reseda luteola* L.	?H				×	×		
DROSERACEAE								
Drosera sp.	G	×	×		×	×		
CRASSULACEAE								
Crassula macrophylla (Hook.f.) Diels & Pritzel	Th			×	×			
C. sieberiana (Schultes) Ostenf.	Th	×	×	×	×	×		×
PITTOSPORACEAE								
Bursaria spinosa Cav.	N-M				×	×		
Cheiranthera linearis A. Cunn.	Ch	×						
Pittosporum phillyraeoides DC.	M				×			
ROSACEAE								
Acaena ovina A. Cunn.	H		×		×	×		
**Alchemilla arvensis* (L.) Scop.	Th			×	×	×		
LEGUMINOSAE								
Acacia acinacea Lindl.	N				×			
A. adunca A. Cunn.	MM	×						
A. armata R. Br.	M	×			×	×		
A. aspera Lindl.	N	×						
A. baileyana F. Muell.	M	×				×		
A. buxifolia A. Cunn.	N	×	×		×	×		
A. decurrens Willd.	M	×	×	×	×	×		
A. difformis R. T. Baker	N or M				×			
A. diffusa Edwards	N	×	×					
A. doratoxylon A. Cunn.	M	×						
A. flexifolia A. Cunn.	N	×						
A. hakeoides A. Cunn.	N or M	×			×			
A. implexa Benth.	M	×			×	×		

Appendix I (*Continued*)

Species	Life Form	Alliance						
		E. dealbata- *E. sideroxylon*	*E. macrorrhyncha-* *E. rossii*	*E. camaldulensis*	*E. woollsiana*	*E. albens*	*E. largiflorens*	*Acacia pendula-* *Atriplex nummularia*
LEGUMINOSAE (*Continued*)								
A. lanigera A. Cunn.	N	×	×					
A. leprosa Sieb.	N	×						
A. lineata A. Cunn.	N	×			×			
A. montana Benth.	N				×	×		
A. obliqua A. Cunn.	N				×			
A. oswaldii F. Muell.	N or M				×			
A. pendula A. Cunn.	M				×		×	×
A. pycnantha Benth.	M	×				×		
A. rubida A. Cunn.	M					×		
A. salicina Lindl.	MM				×			
A. trinerva F. Muell.	N				×			
A. undulifolia Fras.	N				×			
A. verniciflua A. Cunn.	N	×			×			
A. viscidula A. Cunn.	N	×			×			
Cassia eremophila A. Cunn.	M				×			
C. eremophila A. Cunn. var. *zygophylla* Benth.	M				×			
Daviesia corymbosa Sm.	N	×	×					
D. latifolia R. Br.	N	×	×					
Dillwynia floribunda Sm.	N	×			×			
D. juniperina Sieb.	N				×			
Eutaxia microphylla (R. Br.) J. M. Black	N				×			
Glycine clandestina Wendl.	H		×		×	×		
G. latrobeana (Meisn.) Benth.	H					×		
G. tabacina (Labill.) Benth.	H					×		
Hardenbergia violacea (Schneev.) Stearn.	H	×				×		
Indigofera australis Willd.	M	×						
Lotus australis Andr.	Th				×			
**Medicago arabica* (L.) Huds.	Th					×		
**M. denticulata* Willd.	Th			×	×	×	×	×
**M. laciniata* (L.) Mill.	Th					×		×
**M. lupulina* L.	Th					×		
**M. minima* (L.) Bartal.	Th				×	×		×
**M. tribuloides* Desr.	Th				×			×
Pultenaea foliolosa A. Cunn.	N	×						
P. largiflorens F. Muell.	N				×			
Swainsona oncinotropis F. Muell.	H							×
S. oroboides F. Muell.	H							×
S. procumbens F. Muell.	H							×

Appendix I (*Continued*)

Species	Life Form	Alliance						
		E. dealbata- *E. sideroxylon*	*E. macrorrhyncha-* *E. rossii*	*E. camaldulensis*	*E. woollsiana*	*E. albens*	*E. largiflorens*	*Acacia pendula-* *Atriplex nummularia*
LEGUMINOSAE (*Continued*)								
Templetonia egena (F. Muell.) Benth.	M				×			
**Trifolium angustifolium* L.	Th				×	×		×
**T. arvense* L.	Th	×	×		×	×		×
**T. dubium* Sibth.	Th	×	×	×	×	×		
**T. glomeratum* L.	Th	×	×	×	×	×		×
**T. campestre* Shreb.	Th	×	×	×	×	×		
**T. striatum* L.	Th				×	×		
**T. subterraneum* L.	Th	×		×	×	×		
**T. tomentosum* L.	Th				×	×	×	×
GERANIACEAE								
**Erodium botrys* (Cav.) Bertol.	Th			×	×	×		×
**E. cicutarium* (L.) L'Hérit.	Th		×		×	×	×	×
E. cygnorum Nees	Th	×		×	×	×	×	×
**E. moschatum* (L.) L'Hérit.	Th	×		×	×	×	×	×
Geranium pilosum Forst. f.	H	×	×	×	×	×		×
OXALIDACEAE								
**Oxalis cernua* Thunb.	H				×			
O. corniculata L.	H	×	×	×	×	×	×	×
LINACEAE								
Linum marginale A. Cunn.	H				×	×		
ZYGOPHYLLACEAE								
Tribulus terrestris L.	Th				×			×
RUTACEAE								
Geijera parviflora Lindl.	M				×			
Eriostemon trachyphyllus F. Muell.	N	×						
EUPHORBIACEAE								
Beyeria viscosa Miq.	M	×						
Euphorbia drummondii Boiss.	H	×		×	×	×	×	×
E. eremophila A. Cunn.	Th							×
Phyllanthus thymoides Sieb.	N	×	×					
Poranthera microphylla Brongn.	Th		×					

APPENDIX I (*Continued*)

Species	Life Form	Alliance						
		E. dealbata-E. sideroxylon	*E. macrorrhyncha-E. rossii*	*E. camaldulensis*	*E. woollsiana*	*E. albens*	*E. largiflorens*	*Acacia pendula-Atriplex nummularia*
STACKHOUSIACEAE								
Stackhousia monogyna Labill.	G	×			×	×		
SAPINDACEAE								
Dodonaea attenuata A. Cunn.	M				×			
D. boroniaefolia G. Don.	N				×			
D. cuneata Rudge	N	×			×	×		
Heterodendron oleifolium Desf.	M				×			
MALVACEAE								
Lavatera plebeja Sims.	H				×			×
**Malva parviflora* L.	Th				×	×		
**Modiola caroliniana* (L.) G. Don.	H			×		×		
Sida corrugata Lindl.	H			×	×	×	×	×
S. trichopoda F. Muell.	H							×
STERCULIACEAE								
Brachychiton populneus R. Br.	M	×			×	×		
DILLENIACEAE								
Hibbertia linearis R. Br.	N	×	×					
H. sericea (R. Br.) Benth.	N	×	×					
H. stricta R. Br.	N	×						
GUTTIFERAE								
Hypericum gramineum Forst. f.	H	×	×		×	×		
THYMELIACEAE								
Pimelia curviflora R. Br.	N				×			
P. linifolia Sm.	N	×	×					
LYTHRACEAE								
Lythrum hyssopifolia L.	Th				×	×		
MYRTACEAE								
Callistemon sp.	N	×						
Calythrix tetragona Labill.	N	×						
Eucalyptus albens Miq.	M	×			×	×		
E. blakelyi Maiden	M-MM				×	×		

APPENDIX I (*Continued*)

Species	Life Form	Alliance: *E. dealbata*-*E. sideroxylon*	*E. macrorrhyncha*-*E. rossii*	*E. camaldulensis*	*E. woollsiana*	*E. albens*	*E. largiflorens*	*Acacia pendula*-*Atriplex nummularia*
MYRTACEAE (*Continued*)								
E. camaldulensis Dehn.	MM			×	×			
E. cordieri Trabut.	M		×			×		
E. dealbata A. Cunn.	M	×	×			×		
E. dives Schauer.	M		×					
E. dwyeri Maiden & Blakely	M	×						
E. elaeophora F. Muell.	M	×	×			×		
E. largiflorens F. Muell.	M-MM					×		
E. macrorrhyncha F. Muell.	MM	×	×			×		
E. maculosa R. T. Baker	MM	×	×					
E. melliodora A. Cunn.	MM				×	×		
E. polyanthemos Schauer.	MM	×	×					
E. populifolia Hook.	MM				×			
E. rossii Baker & Smith	MM	×	×					
E. sideroxylon A. Cunn.	MM	×						
E. stuartiana F. Muell.	MM					×		
E. woollsiana R. T. Baker	MM	×			×	×		
Kunzea parvifolia Schlech.	N	×						
Leptospermum myrsinoides Schlech.	M		×					
L. stellatum Cav.	N or M	×						
Melaleuca ericifolia Sm.	N	×						
M. pubescens Schau.	M				×			
OENOTHERACEAE								
Epilobium junceum Sol.	Th					×		
**Oenothera biennis* L.	?H				×	×		
HALORAGIACEAE								
Haloragis sp.	H or Ch	×	×			×		
UMBELLIFERAE								
Daucus glochidiatus (Labill.) Fisch. Mey. & Avé -Lall.	Th	×			×	×		×
Eryngium rostratum Cav.	G				×	×		×
Hydrocotyle laxiflora DC.	H or G	×	×		×	×		
EPACRIDACEAE								
Brachyloma daphnoides (Sm.) Benth.	N	×	×					
Leucopogon rufus Lindl.	N	×						

Appendix I (*Continued*)

Species	Life Form	Alliance						
		E. dealbata-E. sideroxylon	*E. macrorrhyncha-E. rossii*	*E. camaldulensis*	*E. woollsiana*	*E. albens*	*E. largiflorens*	*Acacia pendula-Atriplex nummularia*
EPACRIDACEAE (*Continued*)								
L. virgatus (Labill.) R. Br.	N	×						
Lissanthe strigosa (Sm.) R. Br.	N	×	×			×		
Melichrus urceolatus R. Br.	N	×	×					
PRIMULACEAE								
**Anagallis arvensis* L.	Th	×			×	×		
**A. femina* Mill.	Th	×				×		
GENTIANACEAE								
**Erythraea centaurium* (L.) Pers.	Th	×	×		×	×		×
Sebaea ovata R. Br.	Th	×	×					
CONVOLVULACEAE								
Convolvulus erubescens Sims.	H				×	×	×	×
Dichondra repens R. & G. Forster	H	×			×	×		
BORRAGINACEAE								
**Amsinckia hispida* (Ruiz & Pav.) Johnston	Th				×	×		
**Anchusa capensis* Thunb.	?Th				×			
Cynoglossum suaveolens R. Br.	H				×	×		
**Echium italicum* L.	Th				×			
**E. plantagineum* L.	Th	×		×	×	×		
**Heliotropium europaeum* L.	Th			×	×	×		×
Myosotis australis R. Br.	Th	×						
Plagiobothrys elacanthus Johnston	Th				×			×
P. plurisepalus Johnston	Th			×	×			×
LABIATAE								
**Marrubium vulgare* L.	H				×	×		
Mentha gracilis R. Br.	H				×			
**M. pulegium* L.	H				×			
**Salvia verbenacea* L.	H				×	×		
Scutellaria humilis R. Br.	Th		×					
Teucrium racemosum R. Br.	H				×		×	×
SOLANACEAE								
Solanum esuriale Lindl.	Th				×			×
**S. nigrum* L.	Th				×	×		

Appendix I (*Continued*)

Species	Life Form	Alliance						
		E. dealbata- *E. sideroxylon*	*E. macrorrhyncha-* *E. rossii*	*E. camaldulensis*	*E. woollsiana*	*E. albens*	*E. largiflorens*	*Acacia pendula-* *Atriplex nummularia*
SCROPHULARIACEAE								
**Bartschia latifolia* (L.) Sibth. & Sm.	Th		×			×		
**Linaria elatine* (L.) Mill.	Th				×	×		
**L. pelisseriana* (L.) Mill.	Th	×	×		×			
Mimulus gracilis R. Br.	H				×			
M. prostratus Benth.	H				×			
**Verbascum virgatum* Stokes	H				×	×		
Veronica peregrina L.	Th			×			×	×
MYOPORACEAE								
Eremophila longifolia (R. Br.) F. Muell.	M				×			
Myoporum deserti A. Cunn.	N-M	×			×			
M. platycarpum R. Br.	M				×			
PLANTAGINACEAE								
**Plantago lanceolata* L.	H					×		
P. varia R. Br.	H				×	×		×
RUBIACEAE								
Asperula conferta Hook. f.	H				×	×		×
**Galium murale* (L.) All.	Th	×	×		×	×		
**G. parisiense* L. var. *leiocarpum* Tausch.	Th	×	×		×	×		
G. gaudichaudii DC.	H	×				×		
**Sherardia arvensis* L.	Th					×		
CUCURBITACEAE								
**Citrullus vulgaris* Schrad.	Th				×	×		
**Cucumis myriocarpus* Naud.	Th			×	×	×		
CAMPANULACEAE								
Isotoma axillaris Lindl.	?H	×						
Lobelia gibbosa Labill.	Th	×						
Wahlenbergia spp.	Th & H	×	×		×	×		×
GOODENIACEAE								
Goodenia cycloptera R. Br.	H				×			
G. dimorpha Maiden & Betche	H							×
G. glabra R. Br.	H	×			×			
G. hederacea Sm.	H	×			×	×		

APPENDIX I (*Continued*)

Species	Life Form	Alliance						
		E. dealbata-E. sideroxylon	*E. macrorrhyncha-E. rossii*	*E. camaldulensis*	*E. woollsiana*	*E. albens*	*E. largiflorens*	*Acacia pendula-Atriplex nummularia*
GOODENIACEAE (*Continued*)								
G. pinnatifida Schlech.	H	×			×	×		×
G. pusilliflora F. Muell.	Th				×			×
G. subintegra F. Muell.	H				×			×
Velleia paradoxa R. Br.	H					×		
BRUNONIACEAE								
Brunonia australis Sm.	H		×					
COMPOSITAE								
Brachycome ciliaris (Labill.) Less. var. *subintegrifolia* G. L. Davis	Ch				×			
B. goniocarpa Sond. & F. Muell.	Th				×			
B. marginata Benth.	H				×			×
B. marginata Benth. var. *chrysoglossa* F. Muell.	H				×			×
B. muelleroides G. L. Davis	Th							×
B. lineariloba (D.C) Druce	Th				×			×
B. papillosa G. L. Davis	Th							×
Brachycome sp.	Th	×			×	×		
Calocephalus sonderi F. Muell.	Th						×	×
Calotis cuneifolia R. Br.	H or Ch	×			×			
C. hispidula F. Muell.	Th	×			×	×		×
C. scabiosifolia Sond. & F. Muell.	H				×			×
**Carduus pycnocephalus* L.	Th	×	×	×	×	×		
**Carthamus lanatus* L.	Th	×			×	×		×
Cassinia aculeata R. Br.	N	×						
C. arcuata R. Br.	N	×			×			
C. longifolia R. Br.	N	×						
**Centaurea melitensis* L.	Th				×	×		
**C. solstitialis* L.	Th				×	×		
Centipeda cunninghamii (DC.) A. Br. & Aschers.	Th				×		×	×
C. thespidioides F. Muell.	Th				×		×	×
**Chondrilla juncea* L.	G	×			×	×		
**Cichorium intybus* L.	H				×			
**Cirsium lanceolatum* (L.) Scop.	?Th	×	×	×	×	×		×
Cotula australis (Less.) Hook. f.	Th	×		×	×	×		
Craspedia chrysantha Benth.	H							×
C. uniflora Forst. f.	H				×		×	×
**Cryptostemma calendula* (L.) Druce	Th	×	×	×	×	×	×	×

APPENDIX I (*Continued*)

Species	Life Form	Alliance						
		E. dealbata-E. sideroxylon	*E. macrorrhyncha-E. rossii*	*E. camaldulensis*	*E. woollsiana*	*E. albens*	*E. largiflorens*	*Acacia pendula-Atriplex nummularia*
COMPOSITAE (*Continued*)								
Cymbonotus lawsonianus Gaud.	H	×	×		×	×		
Erechtites arguta DC.	Th					×		
E. quadridentata (Labill.) DC.	H	×			×	×		
Eriochlamys behrii Sond. & F. Muell.	Th							×
Gnaphalium japonicum Thunb.	Th	×			×	×		
G. luteoalbum L.	Th					×	×	×
Gnaphaloides uliginosum A. Gray	Th	×			×			
**Hedypnois cretica* (L.) Willd.	Th				×			×
Helichrysum apiculatum (Labill.) DC.	Ch	×	×		×	×		×
H. bracteatum (Vent.) Andrews	Ch	×						
H. obcordatum F. Muell.	Ch	×						
H. semipapposum (Labill.) DC.	Ch	×			×	×		
Helipterum albicans (A. Cunn.) DC.	Th							×
H. albicans (A. Cunn.) DC. var. *auriceps* Ewart	Th							×
H. australe (A. Gray) Druce	Th	×	×		×	×		×
H. corymbiflorum Schlech.	Th				×		×	×
H. jesseni F. Muell.	Th							×
H. laeve (A. Gray) Benth.	Th							×
H. pygmaeum (Benth.) DC.	Th				×	×		×
H. variabile (Sond.) Ostenf.	Th				×			×
**Hypochoeris glabra* L.	Th	×	×	×	×	×		×
**H. radicata* L.	H	×	×	×	×	×		×
Isoetopsis graminifolia Turcz.	Th				×	×		×
**Lactuca scariola* L.	Th				×	×		
Leptorrhynchus panaetioides Benth.	Ch							×
L. squamatus (Labill.) Less.	Ch				×	×		×
L. tetrachaetus (Schlechtd.) J. M. Black	Ch or H				×			
Matricaria discoidea DC.	Th				×			×
Microseris scapigera (Forst. f.) Schultz.-Bip.	Th							×
Minuria denticulata (DC.) Benth.	H				×			
M. leptophylla DC.	H				×			×
Myriocephalus rhizocephalus Benth.	Th				×	×		×
Olearia sp.	N	×						
Olearia tenuifolia Benth.	N	×						
**Silybum marianum* (L.) Gaertn.	Th				×	×		×
Solenogyne belliodes Cass. var. *gunnii* (Hook. f.) G. L. Davis	H		×		×	×		
**Sonchus asper* (L.) Hill.	Th	×			×	×		×

Appendix I (*Continued*)

Species	Life Form	Alliance						
		E. dealbata- *E. sideroxylon*	*E. macrorrhyncha-* *E. rossii*	*E. camaldulensis*	*E. woollsiana*	*A. albens*	*E. largiflorens*	*Acacia pendula-* *Atriplex nummularia*
COMPOSITAE—*continued*								
**S. oleraceus* L.	Th	×		×	×	×	×	×
Stuartina muelleri Sond.	Th	×			×	×		×
Tolpis umbellata Bartol.	Th	×						
Vittadinia triloba (Gaud.) DC.	Ch	×			×	×		×
**Xanthium spinosum* L.	Th				×	×		

Appendix II

NOTES ON THE OCCURRENCE OF SOME SPECIES WITH LIMITED DISTRIBUTION WITHIN THE REGION

Species marked with an asterisk are exotics

Marsilia drummondii A.Br. is confined to wet habitats in the western plains, usually flooded for a period during the winter, with heavy clay soils. It is common in the bottom of gilgais on the grey and brown soils of heavy texture. Elsewhere on the red-brown earths it is found growing chiefly in roadside table-drains where additional water is received as run-off, and the clay subsoil is exposed.

Eragrostis australasica (Steud.) C. E. Hubbard is also confined to wet habitats in the Western Plains. West of the region mapped it may form extensive "cane-grass" swamps, but within the region is found most commonly in roadside table-drains and small depressions within the *Acacia pendula-Atriplex nummularia* Association.

Panicum prolutum F. Muell. is confined to the Western Plains, and requires a more or less wet habitat and heavy soil. It appears to prefer a somewhat shorter period of flooding and better soil aeration than the two previous species. It is common in gilgais, where it occupies an intermediate position between top and bottom of the depression, and along the edges of roadside table-drains.

* *Pennisetum villosum* R.Br. has been recorded only on the roadside at Corowa.

Muehlenbeckia cunninghamii (Meisn.) F. Muell. and *M. diclina* (F. Muell.) J. M. Black both prefer situations subject to winter flooding. They form the "lignum" swamps in depressions on heavy soils of the Western Plains. No extensive areas of lignum swamp have been observed within the region.

* *Rumex roseus* L., on the banks of the Mulwala Irrigation Canal where it crosses the Barooga-Berrigan road.

Atriplex vesicaria Heward ex Benth. occurs only in a protected area at "Coree," 11 miles west of Jerilderie. Extensive communities are well known further west.

Kochia tamariscina (Lindl.) J. M. Black, in a small stand of *Acacia pendula* on heavy grey soil 10 miles east of Narrandera on the Grong Grong road.

Acacia adunca A. Cunn., on immature, light-textured colluvial soil with much undecomposed rock at the northern end of The Rock.

Acacia baileyana F. Muell. has been found growing naturally near Stockinbingal. Newman (1935) has given a full account of its natural distribution. It has also been observed about 7 miles east of Yerong Creek on the road to Mangoplah, but whether it has been introduced into this area is not known.

Acacia flexifolia A. Cunn. In the forest areas between Temora and Ardlethan. It is common in some stands. The soils are immature, with much undecomposed rock, but there has been some profile development.

Acacia salicina Lindl. occurs rarely on sand ridges near Urana and also has been recorded in the cemetery at Jerilderie. It is common on sandy soils to the south of Darlington Point.

Dillwynia juniperina Sieb. occurs 7 miles east of Yerong Creek on the Mangoplah Road. The soil is a yellow podsolic developed on Devonian sediments.

Eutaxia microphylla (R.Br.) J. M. Black occurs near Temora on a sandy loam soil within the red-brown earth group.

Lotus australis Andr. has been recorded only in the cemetery at Culcairn.

Eriostemon trachyphyllus F. Muell. occurs between Temora and Ardlethan.

Dodonaea boroniaefolia G. Don. occurs on shally stony soil on granite between Ardlethan and Temora, and on very shallow soil on sandstone between Morundah and Narrandera.

Hibbertia sericea (R.Br.) Benth., 8½ miles from Cookardinia on the Westby road.

Hibbertia stricta R.Br., 4 miles from Jindera on the Albury road.

Leucopogon rufus Lindl., 9 miles east of Ladysmith on poorly developed stony soil (sedimentary rock).

Leucopogon virgatus (Labill.) R.Br., between Ladysmith and Tarcutta.

Echium italicum L., 3 miles east of Corowa on the Albury road, where it occurs as a roadside weed. It does not make its appearance every year, but the conditions necessary for germination and growth are unknown.

Myoporum deserti A. Cunn. is common north of the Temora-Ardlethan road but seldom found to the south of it.

Cassinia arcuata R.Br., common near Temora and Cootamundra. It has also been recorded between Corowa and Balldale.

Cassinia longifolia R.Br. has been recorded only on the western slopes of the Yambla Range.

* *Cichorium intybus* L., about 10 miles west of Temora.

Craspedia uniflora Forst.f. occurs commonly in the western part of the region in areas subject to flooding. It is commonly seen in or near roadside table-drains. There is a good stand of this species a few miles north of Barooga.

Helichrysum obcordatum F. Muell. in forest areas about 5 miles west of Temora.

Olearia tenuifolia Benth. in forest areas about 5 miles west of Temora.

THE VEGETATION OF THE SOUTH-EASTERN RIVERINA, NEW SOUTH WALES

II. THE DISCLIMAX COMMUNITIES

By C. W. E. Moore*

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Summary

A general description of the disclimax communities in the south-eastern Riverina is presented.

The disclimax communities are essentially the pastures developed on clearing some or all of the trees in the climax communities and grazing the herbaceous stratum. These pastures are discussed in relation to soil and the grazing factor.

Notes on the occurrence of weeds and the possibilities of pasture improvement are given.

I. Introduction

The climax communities of the south-eastern Riverina have been described and mapped in a previous paper (Moore 1953). The general features of the environment (climate, geology, physiography, and soils) were described, and the relationships between the vegetation and the environmental factors were discussed.

The disclimax is defined as a modification of the climax maintained in a relatively stable condition by the activities of man and domestic animals. A discussion of the disclimax communities which have developed after clearing most or all of the trees and grazing of the herbaceous stratum is therefore essentially a discussion of the pastures so developed. In general, clearing has been so extensive that the remaining trees have little or no effect on the growth of the pastures except in their immediate neighbourhood.

The floristic composition and structure of the disclimax communities vary greatly from one stand to another, even within the one association. The many factors responsible for this variation fall into two groups, those related to the climax community and its environment, and those related to the methods and degree of disturbance of the original community. The more important are shown in Table 1.

In the absence of detailed investigations in each community it is not possible to determine precisely the effect of each factor on the development of the disclimax community.

The methods used (Moore 1953) were not such as to permit full segregation of the factors involved, and, under the conditions of the survey, it has

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* Division of Plant Industry, C.S.I.R.O., Canberra, A.C.T.

commonly been necessary to study the effect of the simultaneous operation of more than one factor. Indicators of grazing intensity have been determined chiefly by studies of exclosures (cemeteries and railway embankments), stock routes, travelling stock reserves, and pastures for which stock data were available.

TABLE 1

THE MORE IMPORTANT FACTORS INFLUENCING THE FLORISTIC COMPOSITION AND STRUCTURE OF THE DISCLIMAX COMMUNITIES

Factors Related to the Climax and its Environment	Factors Related to Methods and Degree of Disturbance
1. Floristic composition and structure of the climax	1. Extent of clearing
2. Nature and depth of the soil	2. The grazing animal
3. Steepness of the slope	3. Cultivation
4. Climate	4. Time since interference began and the constancy of the imposed conditions
5. Colonization by native species from neighbouring communities	5. Frequency of fires
	6. Invasion by exotic species

An examination of the vegetation map (Moore 1953) at once shows that the *Eucalyptus woollsiana, E. albens,* and *Acacia pendula-Atriplex nummularia* Alliances occupied the greater part of the region, while the remaining four alliances were of limited occurrence. The disclimax communities of these three alliances are native pastures eminently suited for the grazing of sheep, and a considerable proportion of the area is cultivated for wheat production. A sparse herbaceous stratum develops on clearing the Dry Sclerophyll Forest communities, while the *E. camaldulensis* Alliance and the *E. largiflorens* Alliance occupy relatively small areas. The greatest attention has therefore been paid to the disclimax communities of the Tall Woodland and Shrub Woodland communities.

The genus *Danthonia* is at present under revision by Miss J. W. Vickery of the National Herbarium, Sydney, N.S.W., and no specific names have been used pending publication of her work. The species involved (with the exception of a few found only in ungrazed areas) are closely similar in agronomic and ecological behaviour, all being short-growing perennial grasses of tussock habit.

II. DISCLIMAX COMMUNITIES OF THE DRY SCLEROPHYLL FORESTS

The soils on which the Dry Sclerophyll Forest Subformation develops are always more or less undeveloped, are frequently very shallow, and commonly occur on steep slopes (Moore 1953). They are quite unsuitable for cultivation, and clearing is seldom followed by the development of a reasonable cover of herbaceous species, either native or introduced. Soil erosion usually occurs after removal of the tree stratum, especially where the shrub stratum of the original community was weakly developed. The subsequent establishment of any kind of plant cover becomes extremely difficult.

In these communities, therefore, clearing has seldom been as extensive as in the woodlands, the usual practice being to remove only those trees which provide useful timber or firewood (e.g. *Eucalyptus macrorrhyncha* F. Muell., *E. sideroxylon* A. Cunn. ex Benth., *E. woollsiana* R. T. Baker, and *Callitris glauca* R. Br.) and to leave the remainder more or less intact. No stands have been seen which have not been modified in one way or another. Even where no destruction of the tree stratum has occurred, changes in the subordinate strata have been caused by domestic stock and rabbits.

TABLE 2

SPECIES MOST COMMONLY FOUND IN DISCLIMAX COMMUNITIES OF THE *E. DEALBATA-E. SIDEROXYLON* ALLIANCE

Native Species	Introduced Species
Eucalyptus dealbata A. Cunn.	*Hypochoeris radicata* L.
E. sideroxylon A. Cunn. ex Benth.	*Vulpia bromoides* (L.) S. F. Gray
E. macrorrhyncha F. Muell.	*Aira caryophyllea* L.
Callitris glauca R. Br.	*Trifolium glomeratum* L.
Brachychiton populneus R. Br.	*Erythraea centaurium* (L.) Pers.
Acacia doratoxylon A. Cunn.	*Anagallis arvensis* L.
Cheilanthes tenuifolia Swartz.	
Stypandra glauca R. Br.	
Danthonia spp.	
Stipa falcata Hughes	
Hibberta linearis R. Br.	
Helipterum australe (A. Gray) Druce	
Haloragis sp.	
Phyllanthus thymoides Sieb.	
Lissanthe strigosa (Sm.) R. Br.	
Oxalis corniculata L.	
Brachyloma daphnoides (Sm.) Benth.	
Melichrus urceolatus R. Br.	
Acacia diffusa Edwards	
Crassula sieberiana (Schultes) Ostenf.	
Goodenia hederacea Sm.	

(*a*) Eucalyptus dealbata-E. sideroxylon *Alliance*

The changes in the communities of the *E. dealbata-E. sideroxylon* Alliance have in general been less drastic than those in the Woodland communities except when the more useful members of the dominant stratum have been reduced in numbers. There is little change in the herbaceous stratum, provided grazing by sheep or rabbits is not excessive, as the soils are not suited to the development of herbaceous plants even when the tree and shrub strata are thinned. In some stands partial or complete removal of the dominants may result in the development of a continuous, or almost continuous shrub stratum.

The species most frequently occurring in the disclimax communities are shown in Table 2.

The majority of the species are native, and relatively few exotics are able to establish themselves in these areas. The exotic species commonly found add little to the available sheep feed, as they are widely spaced and poorly grown. It is of interest to note that all except one (*Hypochoeris radicata* L.) are winter-growing annuals.

The poor development of introduced grasses and legumes in the disclimax communities appears to be related primarily to the general low level of soil fertility.

On deep sands of low fertility in the districts of lower rainfall *Aristida jerichoensis* var. *subspinulifera* Henrard may become the dominant species in the herbaceous stratum. Where rainfall is relatively high *Aristida ramosa* R. Br. becomes the dominant on similar soils.

(*b*) Eucalyptus macrorrhyncha-E. rossii *Alliance*

The factors affecting the development of these communities are in general similar to those affecting the development of the disclimax communities in the *E. dealbata-E. sideroxylon* Alliance. There is, however, a greater tendency to the development of a herbaceous stratum, especially in cleared stands of the *E. macrorrhyncha-E. polyanthemos* Association, because of the higher rainfall and the deeper and more mature soils. The herbaceous stratum is nevertheless not strongly developed, though a pasture of low carrying capacity may be induced. There is commonly a tendency to the development of *Aristida ramosa* as the dominant pasture species in such areas unless light grazing is practised. In these communities there is usually a shrub stratum consisting of small shrubs which provide a certain amount of coarse feed for sheep. The most commonly occurring species are *Lissanthe strigosa, Hibbertia linearis,* and *Melichrus urceolatus.*

Most of the communities of this alliance are, like those of the *E. dealbata-E. sideroxylon Alliance,* relatively uncleared, and little or no pasture is developed. The most commonly occurring species in the disclimax communities are given in Table 3.

(*c*) *Development of Improved Pastures in the Dry Sclerophyll Forest Subformation*

No improved pastures have been seen in any area cleared from Dry Sclerophyll Forest. However, it appears likely that, at least on the deeper soils where the slope is not too steep and where rainfall is adequate, high-producing pastures of *Phalaris tuberosa* L. or Wimmera ryegrass with subterranean clover could be developed. Anderson and Moye (1952) have shown that in similar situations on the Southern Tablelands excellent results may be obtained with these species if sufficient superphosphate, a small dressing of ammonium molybdate, and, on the more acid soils, a light dressing of lime, are applied.

III. DISCLIMAX COMMUNITIES OF THE TALL WOODLANDS

The disclimax communities of the Tall Woodlands are pastures in which the dominant perennial species are *Stipa falcata* and *Danthonia* spp.

TABLE 3

SPECIES MOST COMMONLY FOUND IN DISCLIMAX COMMUNITIES OF THE *E. MACRORRHYNCHA-E. ROSSII* ALLIANCE

Native Species	Introduced Species
Eucalyptus macrorrhyncha F. Muell.	*Trifolium glomeratum* L.
E. polyanthemos Schau.	*Erythraea centaurium* (L.) Pers.
E. rossii Baker & Smith	*Hypochoeris radicata* L.
E. maculosa R. T. Baker	*Kohlrauschia prolifera* (L.) Kunth.
E. eleaophora F. Muell.	*Vulpia bromoides* (L.) S. F. Gray
Hibbertia linearis R. Br.	*Bromus mollis* L.
Lissanthe strigosa (Sm.) R. Br.	*Aira caryophyllea* L.
Cheilanthes tenuifolia Swartz.	*Trifolium campestre* Shreb.
Melichrus urceolatus R. Br.	*Trifolium arvense* L.
Hypericum gramineum Forst. f.	
Danthonia spp.	
Stipa falcata Hughes	
Panicum effusum R. Br.	
Hydroctyle laxiflora DC.	
Oxalis corniculata L.	
Aristida ramosa R. Br.	
Helipterum australe (A. Gray) Druce	
Acacia buxifolia A. Cunn.	
Acacia decurrens Willd.	
Daviesia latifolia R. Br.	
Acacia diffusa Edwards	

(*a*) E. woollsiana *Alliance*

In the climax communities of this alliance the shrub stratum is weakly developed or absent, while the herbaceous stratum, though commonly weakly developed, is dominated by grasses. In communities in which *Callitris glauca* is a codominant, the herbaceous stratum was probably less well developed than in those in which this species was absent or occasional. The evidence of cemeteries and railway embankments suggests that the dominant species in the herbaceous stratum of the original communities (at least the more open ones) were tall grasses, of which three species may be seen in exclosures, viz. *Themeda australis* (R. Br.) Stapf., *Stipa aristiglumis* F. Muell., and less commonly *Poa australis* R. Br. Sturt's references to "Forest Grass" (Sturt 1834) suggest a tall grass, though it seems likely that he used this term for a number of species. Under normal conditions of grazing, neither *T. australis* nor *P. australis* is to be found in the pastures, but *S. aristiglumis* may occur as an occasional species in areas not subjected to heavy grazing. All three species have been observed on little-used stock routes, *S. aristiglumis* being much more common than the other two.

When the trees are thinned or completely cleared and grazing by sheep is practised, the usual dominants are *Stipa falcata* and *Danthonia* spp., which provide a good perennial cover provided grazing is not too severe.

In Table 4 species with a presence (P) value greater than 20 are listed. This value has been defined by Curtis and McIntosh (1950) as follows:

$$\text{Presence} = \text{P} = \frac{\text{No. of stands in which a species occurs}}{\text{Total No. of stands examined}} \times 100.$$

The almost universal occurrence of *Stipa falcata* and *Danthonia* and the relative importance of introduced winter-growing annuals are made clear in Table 4.

TABLE 4

SPECIES (OTHER THAN TREES) WITH PRESENCE VALUES GREATER THAN 20 IN ALL STANDS EXAMINED WITHIN THE *E. WOOLLSIANA* ALLIANCE

Native Species	P	Introduced Species	P
Stipa falcata Hughes	96	*Trifolium glomeratum* L.	65
Danthonia spp.	95	*Cryptostemma calendula* (L.) Druce	63
Chloris truncata R. Br.	76	*Hordeum leporinum* Link.	47
Sida corrugata Lindl.	68	*Vulpia bromoides* (L.) S. F. Gray	45
Euphorbia drummondii Boiss.	50	*Hypochoeris radicata* L.	43
Chenopodium carinatum R. Br.	45	*Carthamus lanatus* L.	42
Vittadinia triloba (Gaud.) DC.	43	*Trifolium arvense* L.	40
Wahlenbergia spp.	38	*Sonchus oleraceus* L.	33
Erodium cygnorum Nees	37	*Trifolium subterraneum* L.	32
Aristida behriana F. Muell.	34	*Eragrostis cilianensis* (All.) Link ex Lutnai	32
Convolvulus erubescens Sims	33	*Erodium moschatum* (L.) L'Hérit.	28
Panicum effusum R. Br.	29	*Medicago denticulata* Willd.	21
Crassula sieberiana (Schultes) Ostenf.	28		
Agropyron scabrum (R. Br.) Beauv.	26		
Dichopogon strictus (R.Br.) J. G. Baker	26		
Helipterum australe (A. Gray) Druce	24		
Cynodon dacyton (L.) Pers.	24		
Chloris acicularis Lindl.	22		
Lepidium hyssopifolium Desv.	22		
Trichinium spp.	22		
Chenopodium pseudomicrophyllum Aellen	21		
Kochia crassiloba R. H. Anderson	21		

The dominant species in the pastures, and also many of the subordinate species, differ according to soil texture and grazing intensity.

(i) *Pastures of the Light-textured Soils.*—The light-textured soils are deep sands and sandy loams, the depth of the A horizon being more than 4 in. *Stipa falcata* is the dominant pasture species on these soils under light to moderate grazing. *Eragrostis elongata* (Willd.) Jacq. has occasionally been observed on deep sands as a common species under conditions of infrequent light grazing or in the absence of sheep. *Danthonia* spp. are never prominent on these soils, even under the most lenient grazing treatment. These species appear to require a relatively high proportion of clay in the soil for best development, and prefer soils with a more or less compact surface.

The first effect of increasing grazing intensity on these pastures is the complete removal of *Danthonia* spp. The danthonias are more palatable than *Stipa falcata,* and on the light-textured soils are readily grazed out by sheep. Further increases in grazing intensity reduce the proportion of *Stipa falcata,* and there is frequently an increase in the proportion of *Panicum effusum* at this stage. However, the most obvious result of a decrease in *S. falcata* is an increase in the proportion of annuals, the most common of which are *Erodium cygnorum, E. moschatum, Hordeum leporinum, Cryptostemma calendula, Bromus mollis,* and *Bromus rigidus* Roth. *Heliotropium europaeum* L. may be an important summer-growing annual when the perennial grasses have been weakened.

Severe grazing on the deep sands may result in the weakening of *S. falcata* to such an extent that bare areas develop, especially on the tops of the hills, and the sand may begin to drift.

(ii) *Pastures of the Heavier-textured Soils.*—This group includes loams and clay loams and also soils with a sandy to sandy loam A horizon, provided it is not more than 3-4 in. deep, and has a compact surface. Under these conditions the roots of the plants readily penetrate the clay B horizon.

The dominant pasture species on these soils is most commonly *Danthonia,* though *Stipa falcata* may be codominant in the more lightly grazed areas.

Increasing the grazing intensity on the pastures of the heavier-textured soils always causes a decrease in the proportion of *S. falcata* and an increase in that of *Danthonia.* A number of measurements of the basal area of the perennial grasses were made on this type of pasture. Under conditions of light to moderate grazing the mean percentage basal areas of *Stipa falcata* and *Danthonia* were 2.4 and 0.8 per cent. respectively, while under conditions of heavy grazing the mean basal area of *S. falcata* was 0.6 per cent. and that of *Danthonia* 3.7 per cent. It commonly happens that under moderate grazing the basal area of the *Danthonia* is greater than the total basal area of the *Danthonia* and *Stipa* under conditions of light grazing. The type of *Danthonia* persisting under moderate to heavy grazing is a very short grass, probably with a lower total production than the taller types found in lightly grazed pastures.

The development of annuals appears to depend on the precise soil conditions. If the grazing intensity is such as to weaken the *Danthonia* sward, winter annuals become dominant where the surface soil is not too strongly compacted. These include *Hordeum leporinum, Erodium cygnorum, Medicago denticulata,* and *Trifolium glomeratum.* When the compaction of the surface soil is such that annual species cannot readily germinate and establish, weakening of the *Danthonia* sward results in the development of more or less extensive bare areas or scalds, the reclamation of which is usually difficult and slow.

Chloris truncata R. Br. is a common minor constituent of the pastures, but in overgrazed areas may, in a suitable season (wet summer) become the dominant species. It usually behaves as a short-lived perennial, but when it becomes dominant during a wet summer the majority of plants behave as annuals.

There are few summer-growing species suited to the area because of the unfavourable summer rainfall. The only important summer-growing grasses are *Panicum effusum* and *Chloris truncata* which become prominent only during wet summers. Two summer-growing annuals, *Heliotropium europaeum* and *Chenopodium carinatum*, occur commonly but both require a weakening of the perennials and adequate summer rains.

(iii) *Weeds.*—Weakening of the pasture by the removal of a large proportion of the perennial grasses not only allows invasion by winter annuals of some grazing value, but also permits invasion of the pastures by weed species. The most frequently occurring weeds are annuals, with the exception of *Chondrilla juncea* L. (skeleton weed). This species does not become a pest in grazed pastures, though it may frequently form such a dense stand in a wheat paddock that harvesting of the crop becomes impossible.

Carthamus lanatus (saffron thistle) is a common species throughout the communities of the *E. woollsiana* Alliance, but develops dense stands most commonly on the heavier-textured soils after weakening of the perennials by cultivation or overgrazing. Its development appears to depend in part on seasonal conditions, since dense stands are much more common in some seasons than in others.

Salsola kali L. may become prominent in overgrazed areas in the drier districts, but is seldom a serious weed.

The only important summer-growing weed is *Heliotropium europaeum*, which has been found to cause serious losses of sheep (Anon. 1949). It is widespread in the *E. woollsiana* Alliance, but flourishes only in the absence of competing plants. It therefore becomes prominent chiefly where the perennial species in the pasture have been seriously weakened or eliminated by cultivation or overgrazing. A good sward of perennial grasses will prevent the development of dense stands of this species (Plate 1, Figs. 1 and 2).

(iv) *Pasture Improvement.*—Because of the relatively low rainfall over the greater part of the country occupied by the *E. woollsiana* Alliance, there has been little development of improved pastures, except in the irrigation areas. There seems little doubt, however, that much greater use could be made of sown pasture species in both the lower- and higher-rainfall districts.

Subterranean clover (chiefly the Mulwala strain) has been successfully grown for many years in the Murray Valley from Corowa to Mulwala. The clover has frequently appeared in the pastures of this district as a volunteer species, and has been encouraged by many farmers by the application of superphosphate. Wimmera ryegrass can also be successfully grown in this district, and there seems little doubt that it could be used further west without irrigation on many soils. Successful establishment of this species has been seen on a sandy soil near Urana (mean annual rainfall 17 in.). The natural pasture (in which *Danthonia* and *Stipa falcata* were the dominant species) was lightly harrowed with the disc harrows in order to maintain a proportion of the native grasses while at the same time providing a satisfactory seed-bed for the Wimmera ryegrass, which was sown with a drill. When this area was inspected 4 years after establishment, there was still a good stand of Wimmera ryegrass.

It is possible that even better results would be obtained by the use of an early-maturing strain of subterranean clover in conjunction with the ryegrass.

The use of *Phalaris tuberosa* has not become widespread. This species can be grown in areas with a mean annual rainfall in excess of 19 in. A *Phalaris* pasture has been established between Corowa and Mulwala, but this is the only one observed by the author within the *E. woollsiana* Alliance.

Though it is probable that it will be necessary to rely to a large extent on the native grasses in this region, the possibilities of introduced pasture species have not yet been thoroughly investigated.

(*b*) E. albens *Alliance*

(i) *General Description of the Pastures.*—The climax communities of this alliance were similar in structure to those of the *E. woollsiana* Alliance in that the shrub stratum was weakly developed or absent. It is probable, however, that there was generally a better development of the herbaceous stratum. The evidence of the early explorers (see Sturt 1834; Hovell and Hume 1837; Andrews 1920) suggests that the herbaceous stratum was well developed and that the dominant species was *Themeda australis.* This species is common in exclosures such as cemeteries (Plate 2, Fig. 1) and railway embankments, and along roadsides where travelling stock seldom graze. Other tall grasses found in ungrazed or very lightly grazed areas include *Stipa aristiglumis* and *Poa australis.*

In the disclimax communities the most common pasture dominants are *Stipa falcata, S. variabilis,* and *Danthonia* spp. Since the soil parent materials are commonly granites and sandstones, the surface soil is frequently of a more or less sandy texture, and there is a marked dominance of *Stipa* species in the more lightly grazed areas. Introduced legumes are common but usually poorly developed and contribute little to the total production. They are more prominent within the *E. albens-E. melliodora-E. blakelyi* Association than within the *E. albens* Association.

Summer-growing species are not generally abundant in the pastures. They include *Panicum effusum* and *Chloris truncata.* Summer-growing annual herbs are rare.

Those species with a presence value greater than 20 are listed in Table 5.

Since the *E. albens* Alliance is in general confined to areas of higher rainfall than the *E. woollsiana* Alliance, changes in soil texture have a less marked effect on the composition of the pastures. However, the rolling to hilly nature of the topography provides two distinct habitats, one in the valleys and the other on the hills. The soils of the former are deeper, more highly leached, and always better watered (through run-off from the surrounding country) than the soils of the hills. The composition of the pastures of the valleys is consequently usually different from that of the slopes. In general, the same species are present in both habitats, but introduced annuals (*Hordeum leporinum, Vulpia bromoides, Bromus rigidus, B. mollis, Trifolium glomeratum, T. arvense, T. dubium, T. campestre, Medicago minima, Cryptostemma calendula,* etc.) are generally more abundant, and the perennial species are commonly less abundant in the valleys than on the hills.

(ii) *Effect of Grazing on the Composition of the Pastures.*—The general effect of increasing grazing intensity on the pastures developed within the *E. albens* Alliance is similar to that for the pastures on the medium to heavy-textured soils in the *E. woollsiana* Alliance. In ungrazed areas tall grasses such as *Themeda australis, Stipa aristiglumis,* and *Poa australis* are the usual dominants. One area grazed by cattle only has been observed in which *T. australis* is the dominant pasture species. None of these species is capable of withstanding continuous moderate to heavy grazing by sheep, and they are either absent from grazed pastures or are present as rare species only.

TABLE 5

SPECIES (OTHER THAN TREES) WITH A PRESENCE VALUE GREATER THAN 20 IN ALL STANDS EXAMINED WITHIN THE *E. ALBENS* ALLIANCE

Native Species	P	Introduced Species	P
Danthonia spp.	95	*Trifolium glomeratum* L.	81
Stipa falcata Hughes	88	*Vulpia bromoides* (L.) S. F. Gray	74
Agropyron scabrum (R. Br.) Beauv.	67	*Hypochoeris radicata* L.	59
Chloris truncata R. Br.	60	*Trifolium arvense* L.	57
Oxalis corniculata L.	59	*Carthamus lanatus* L.	55
Panicum effusum R. Br.	55	*Cryptostemma calendula* (L.) Druce	50
Dichopogon strictus (R.Br.) J. G. Baker	55	*Hordeum leporinum* Link.	43
Lomandra spp.	55	*Trifolium campestre* Shreb.	43
Aristida behriana F. Muell.	48	*Kohlrauschia prolifera* (L.) Kunth.	43
Themeda australis (R. Br.) Stapf.	47	*Trifolium dubium* Sibth.	40
Helipterum australe (A. Gray) Druce	45	*Salvia verbenacea* L.	38
Vittadinia triloba (Gaud.) DC.	45	*Bromus mollis* L.	36
Bothriochloa ambigua S. T. Blake	40	*Trifolium subterraneum* L.	31
Wahlenbergia spp.	40	*Chondrilla juncea* L.	29
Stipa variabilis Nees	40	*Hypochoeris glabra* L.	29
Rumex brownii Campd.	33	*Sonchus oleraceus* L.	29
Dianella laevis R. Br.	31	*Erythraea centaurium* (L.) Pers.	24
Hydrocotyle laxiflora DC.	31	*Aira caryophyllea* L.	24
Helichrysum apiculatum (Labill.) DC.	29	*Medicago denticulata* Willd.	24
Cymbonotus lawsonianus Gaud.	29	*Medicago minima* (L.) Bartal.	24
Poa australis R. Br.	26	*Echium plantagineum* L.	24
Stuartina muelleri Sond.	26		
Daucus glochidiatus (Labill.) Fisch. Mey. et Avé-Lall.	24		
Erodium cygnorum Nees	24		
Aristida ramosa R. Br.	21		
Euphorbia drummondii Boiss.	21		

Under light to moderate sheep grazing, the pasture dominants are mid grasses (usually *S. falcata* and some types of *Danthonia*) with a significant proportion of short grasses (e.g. *Danthonia, C. truncata, P. effusum,* and *Aristida behriana*), while under moderate to severe grazing the *Stipa* is weakened, and short forms of *Danthonia* take possession. Further increases in the grazing intensity cause a weakening of the *Danthonia* and invasion by annuals.

In pastures which have at some period been subjected to overgrazing, *Bothriochloa ambigua* may become dominant. This species forms a dense turf in which other species have difficulty in establishing themselves. A common feature is the development of alternes of *Danthonia* and *Bothriochloa* dominance (Plate 2, Fig. 2).

(iii) *Weeds.*—A common weed in the pastures throughout the Alliance is *Carthamus lanatus* and in some seasons dense stands develop following overgrazing and cropping.

A weed of considerable importance on the deep alluvial soils associated with rivers and creeks is *Silybum marianum* (L.) Gaertn. (variegated thistle). The total area involved is relatively small, but the soils are always deep alluvials of high fertility and under proper management could produce large quantities of fodder. Invasion by *S. marianum* could be prevented by the use of high-producing perennial pasture species such as lucerne or *Phalaris tuberosa.* The erosion of these valuable areas of fertile soil would also be checked by the establishment of a good cover of perennial species.

An extensive area of river flat frequently occupied by variegated thistle can be seen on the Murrumbidgee flats to the south of Gundagai. The thistles were particularly dense and well grown in early December 1951 when no fences could be seen and cattle grazing amongst them were completely hidden. The value of lucerne for such areas was clearly demonstrated at this time. One small paddock of lucerne was completely free of the weed except in a narrow border near the fence where it had not been possible to cultivate and sow lucerne.

Chondrilla juncea may be a serious pest in cultivated areas, but under sheep-grazing is not an important species, though it is usually a minor constituent of the pastures.

Heliotropium europaeum may become prominent under favourable conditions (a weak perennial sward and high summer rainfall) but it seldom attains a density equal to that in some of the more heavily grazed pastures of the *E. woollsiana* Alliance, especially in the Murray Valley.

(iv) *Pasture Improvement.*—Relatively few areas of improved pastures are seen within the *E. albens* Alliance. Over practically the whole area the mean annual rainfall is greater than 19 in., the soils are deep podsolics, and the slopes are, with relatively few exceptions, not such as to make the introduction of pasture species impracticable. Subterranean clover, Wimmera ryegrass, and *Phalaris tuberosa* could be used over the greater part of the area. Phosphatic fertilizer is essential to the satisfactory establishment of these species.

IV. Disclimax Communities of the Savannah Woodlands

(*a*) E. largiflorens *Alliance*

The *E. largiflorens* Alliance occupies only a very small area within the region to the west of Jerilderie, and little useful general information can be obtained about the disclimax communities. Beadle (1948) has described the pastures of this community in some detail. In the few stands examined in the region the most abundant species are *Danthonia* and *Kochia ciliata* F. Muell.

(*b*) E. camaldulensis *Alliance*

Beadle (1948) has discussed the effect of thinning or clearing *E. camaldulensis* Dehn. forest communities on the development of pasture species. In narrow belts of *E. camaldulensis* along the smaller streams, it commonly happens that no pasture is developed, either because the ground is normally flooded for long periods during the winter or because the stream banks are too steep for the development of a pasture (e.g. in many parts of Billabong Creek). Where the topographic conditions are favourable the type of pasture would appear to depend primarily on soil type and drainage. Where the drainage is poor, and the soil is waterlogged for long periods, the dominant pasture species is *Amphibromus neesii* Steud. with few associated species.

On well-drained sites the predominant pasture species are usually annuals, with a sparse cover of perennial grasses, chiefly *Danthonia.* The most abundant annuals include *Hordeum leporinum, Bromus mollis, B. rigidus, Vulpia bromoides, Medicago denticulata, Trifolium glomeratum,* and *Erodium moschatum.*

The pastures developed within the *E. camaldulensis* Alliance are in general of low carrying capacity. A number of areas have been observed where subterranean clover has been introduced, and there seems little doubt that this species could be more widely used in well-drained areas not subjected to long periods of flooding.

On a deep, sandy soil on Yanko Creek to the north of Jerilderie (mean annual rainfall about 15 in.), an excellent stand of Wimmera ryegrass has been established without the use of fertilizers. The Wimmera ryegrass was drilled into the natural pasture with a combine. Subterranean clover has not been used in this area.

Further improvement of the pastures in many areas could be achieved by the use of *Phalaris tuberosa* or Wimmera ryegrass in conjunction with subterranean clover.

V. Disclimax Communities of the Shrub Woodlands (Acacia pendula-Atriplex nummularia Alliance)

In a previous paper (Moore 1953) evidence was presented showing that the apparent grasslands occurring principally to the north and west of Urana are disclimax communities developed after the destruction of *Acacia pendula* A. Cunn. and *Atriplex nummularia* Lindl. The former species has been allowed to regenerate in a few small areas by the exclusion of stock, but east of Yanko Creek *Atriplex nummularia* can now be found only in two small areas where it has been carefully preserved. The type of pasture developed depends on two factors, the soil and the intensity of grazing.

Within the *Acacia pendula-Atriplex nummularia* Alliance two major groups of soil occur. The red-brown earths occupy the higher levels, and are well-drained soils, having a shallow A horizon of sandy loam to loam. The grey and brown soils of heavy texture occur at lower levels, and are commonly clays or clay loams with a uniform grey or brown colour throughout the profile, varying amounts of lime, and frequently with gypsum in the illuvial horizons.

The topography is flat and the difference in level between the two groups of soil may be only a few inches. Drainage on the heavy soils is impeded, and they frequently, though not invariably, show gilgai formations.

TABLE 6

SPECIES WITH A PRESENCE VALUE GREATER THAN 20 IN ALL STANDS EXAMINED WITHIN THE *ACACIA PENDULA-ATRIPLEX NUMMULARIA* ALLIANCE

Native Species	P	Introduced Species	P
Danthonia spp.	100	*Medicago denticulata* Willd.	89
Chloris truncata R. Br.	95	*Hordeum leporinum* Link.	68
Stipa falcata Hughes	81	*Carthamus lanatus* L.	54
Sida corrugata Lindl.	73	*Sonchus oleraceus* L.	51
Kochia ciliata F. Muell.	68	*Salsola kali* L.	49
Atriplex semibaccata R. Br.	57	*Trifolium glomeratum* L.	43
Plantago varia R. Br.	54	*Cryptostemma calendula* (L.) Druce	43
Asperula conferta Hook. f.	51	*Vulpia bromoides* (L.) S. F. Gray	38
Goodenia pusilliflora F. Muell.	49	*Medicago tribuloides* Desr.	35
Crassula sieberiana (Schultes) Ostenf.	49	*Hypochoeris radicata* L.	27
Stipa aristiglumis F. Muell.	49	*Microseris scapigera* (Forst. f.) Schultz-Bip.	24
Myriocephalus rhizocephalus Benth.	43	*Hypochoeris glabra* L.	22
Daucus glochidiatus (Labill.) Fisch. Mey. & Avé-Lall.	43	*Erodium cicutarium* (L.) L'Hérit.	22
Brachycome lineariloba (DC.) Druce	41		
Calotis scabiosifolia Sond. & F. Muell.	41		
Helipterum corymbiflorum Schlech.	41		
Oxalis corniculata L.	41		
Spergularia rubra (L.) J. & C. Presl.	41		
Chloris acicularis Lindl.	38		
Helipterum pygmaeum (Benth.) DC.	38		
Helipterum variabile (Sond.) Ostenf.	35		
Trichinium spp.	35		
Anguillaria dioica R. Br.	32		
Hypoxis pusilla Hook. f.	32		
Erodium cygnorum Nees	32		
Kochia crassiloba R. H. Anderson	30		
Helipterum australe (A. Gray) Druce	30		
Eragrostis parviflora (R. Br.) Trin.	30		
Solanum esuriale Lindl.	27		
Kochia excavata J. M. Black	27		
Bulbine bulbosa (R. Br.) Haw.	27		
Sporobolus caroli Mey.	27		
Swainsona spp.	25		
Calocephalus sonderi F. Muell.	24		
Teucrium racemosum R. Br.	24		
Vittadinia triloba (Gaud.) DC.	24		
Panicum prolutum R. Br.	22		
Alternanthera denticulata R. Br.	22		
Arthropodium minus R. Br.	22		
Bassia quinquecuspis F. Muell.	22		
Centipeda cunninghamii (DC.) R. Br. & Aschers, and *C. thespidioides* F. Muell.	22		
Helichrysum apiculatum (Labill.) DC.	22		

The dominant perennials in the pastures under ordinary grazing conditions are species of *Stipa* and *Danthonia.* There is a greater variety of commonly occurring subordinate species in these pastures than in any other disclimax communities within the region. Table 6 lists species with a presence value greater than 20 for all stands examined.

The pastures developed on the red-brown earths differ in dominant species and to some extent in subordinate species from those developed on the grey and brown soils of heavy texture. Those of the former group will be described as the pastures of the light-textured soils, and those of the latter as the pastures of the heavy-textured soils.

(*a*) *Pastures of the Light-textured Soils*

Under conditions of very light grazing, particularly if the area is grazed intermittently by young sheep only, *Kochia aphylla* R. Br. is a prominent constituent of the disclimax, sometimes reaching the status of a dominant species (Plate 3, Fig. 1). Under these conditions *Danthonia* is usually the principal grass, though examples have been seen where *Hordeum leporinum* is a prominent winter constituent. Other annual species, both indigenous and exotic, are of little importance in these pastures, though many species may be present. On the more sandy soils *Stipa falcata* may be codominant with *Danthonia.*

With increasing grazing intensity *Kochia aphylla* disappears, the proportion of *Stipa falcata* is reduced, and that of *Danthonia* increased. At this stage there may not be any increase in the proportion of annuals, since the space previously occupied by *Kochia* and *Stipa* is occupied by *Danthonia. Stipa aristiglumis* may be present as an occasional species.

Further increases in the grazing intensity cause a reduction in the proportion of *Danthonia* and an increase in *Chloris truncata,* which under conditions of severe grazing may become the dominant species. There is also an increase in the proportion of annuals, which may include species of grazing value such as *Erodium cygnorum, Hordeum leporinum, Medicago denticulata,* and *Trifolium glomeratum,* but frequently the annuals consist chiefly of native species of little or no grazing value, the most common of which include *Helipterum pygmaeum, H. variabile, H. albicans,* various species of *Brachycome,* and *Calotis hispidula* F. Muell.

On the more sandy areas where *Stipa falcata* is dominant under conditions of light grazing, reduction of this species is not followed by a proportionate increase in *Danthonia,* and the change to dominance by annuals is more rapid.

Severe grazing may result in the complete elimination of the perennial grasses, when extensive scalds (bare areas) develop.

(*b*) *Pastures of the Heavy-textured Soils*

Under light to moderate grazing, the dominant pasture species is *Stipa aristiglumis,* especially on soils with a self-mulching surface and those showing gilgai formation (Plate 3, Fig. 2; Plate 4, Fig. 1). This species also occurs, however, in lightly grazed areas of the more compact heavy-textured soils. *Danthonia* is prominent on the shelf, and S. *aristiglumis* on the puff. The depressions may be occupied by a series of plants throughout the year according to the season. In the winter, when the depressions may be filled with water, or the soil is saturated, *Marsilia drummondii* A. Br. is prominent. As the water dries out other more xeric species colonize the area. These are usually annuals, and include *Hordeum leporinum*, *Medicago* spp., and *Carthamus lanatus*. These introduced annuals are usually widespread in these areas.

Other common associated species in the pastures include *Panicum prolutum* F. Muell. (especially between the top and bottom of the depressions), *Atriplex semibaccata*, and numerous endemic ephemerals, such as *Helipterum* spp., *Calotis* spp., and other composites, *Bassia* spp., and *Kochia* spp.

Heavy and severe grazing cause the reduction and finally the elimination of *Stipa aristiglumis*. If the grazing intensity is not too severe, *Danthonia* becomes the dominant perennial except on the puffs and in the depressions, in which introduced annuals predominate. *Chloris truncata* becomes more prominent, finally becoming the dominant species on the most heavily grazed areas. There is an increase in the proportion of annuals, the most abundant being *Hordeum leporinum*, *Erodium cygnorum*, *Medicago denticulata*, *Medicago tribuloides*, and *Carthamus lanatus*.

On the more compact soils heavy to severe grazing results in the development of a low-producing pasture in which *Danthonia* is a minor species only, *Chloris truncata* is the dominant grass, and the annuals consist chiefly of native species of little or no grazing value such as *Calotis scabiosifolia*, *Helipterum corymbiflorum*, *Brachycome* spp., and *Kochia ciliata*.

(*c*) *Weeds*

No weeds of major economic importance occur in the pastures of the *Acacia pendula-Atriplex nummularia* Alliance. *Carthamus lanatus* occurs commonly throughout the community but seldom becomes dominant on large areas. *Heliotropium europaeum* has been observed occasionally, but in no instance has it been seen as the dominant species during the summer. *Salsola kali* and *Bassia quinquecuspis* may occur in severely grazed pastures, but do not become serious pests.

(*d*) *Pasture Improvement*

There are very few areas in which any attempt at pasture improvement has been made. There are indications, however, that Wimmera ryegrass may have some value in this part of the region. It is frequently seen, especially on roadsides but also in grazed pastures, as a common species on the self-mulching grey and brown soils of heavy texture, and it is on these soils in particular that it may be possible to replace *Hordeum leporinum* with this species. If this could be achieved the damage to sheep caused by the seed of *Hordeum leporinum* would be overcome.

On a property near Jerilderie Wimmera ryegrass has been drilled into the pastures on red-brown earths with a compact surface, and a considerable degree of success has been achieved in the reduction of *Hordeum leporinum*. Whether the ryegrass will re-seed successfully over a period of years has yet to be determined.

The general changes, in the pastures following grazing by sheep, weed invasion, and the possibilities of pasture improvement with natural rainfall, are summarized for each alliance in Table 7.

IV. Discussion

The dominant perennial species in the pastures throughout the region are species of *Stipa* and *Danthonia*. In all communities there is the same kind of change in the dominant species as the grazing intensity is increased. In ungrazed or very lightly grazed areas tall grasses predominate. These are most typically represented by *Stipa aristiglumis, Themeda australis,* and *Poa australis.* With moderate grazing these are replaced by mid grasses, represented most frequently by *Stipa falcata* and some species of *Danthonia.* Heavy and severe grazing causes a reduction of the mid grasses and their replacement by short grasses (*Chloris truncata* and some species of *Danthonia*), and a marked increase in the proportion of annuals.

Beadle (1948), discussing the effect of grazing on the pastures in the *E. woollsiana* Alliance, states that "the first plant to disappear from the stable pastures is *Danthonia.*" Moore (1940) has stated that "the proportion of *Danthonia* to *Stipa* decreases . . . . . where overstocking is practised." Biddiscombe (1953) has shown that in the *Stipa-Danthonia* pastures in the Trangie district increasing grazing intensity has little effect on the percentage of *Danthonia,* but that there is actually a slight increase in the more heavily grazed pastures.

The reaction of the Danthonias to grazing appears to depend on a number of factors, including the species (perhaps the ecotype) concerned, soil texture, incidence of rainfall, and the type of stock and intensity of grazing. The taller-growing species (or ecotypes) withstand light to moderate grazing by sheep, especially when grazing is not continuous, and may be abundant in areas grazed by cattle only. On deep sands and on self-mulching clays and clay loams, *Danthonia* spp. do not usually become dominant, and are quickly reduced under sheep-grazing. When the soil has a compact surface the proportion of *Danthonia* is usually increased as the intensity of grazing by sheep increases, though the tall forms are replaced by short, low-producing forms. Severe grazing of a *Danthonia*-dominant pasture may result in invasion by *Chloris truncata* and winter-growing annuals or in the development of extensive scalds. Where there is a relatively high incidence of summer rainfall (as at Trangie) competing summer grasses suppress the development of *Danthonia* spp.

Bothriochloa ambigua may become a dominant species in heavily grazed pastures within the *Eucalyptus albens* Alliance. An examination of the soils where alternes of *Danthonia* and *B. ambigua* have developed suggested that the latter species invades areas where the A_1 horizon has been lost by erosion, since the present surface soil is similar to the A_2 horizon of contiguous areas where *Danthonia* is the dominant pasture species. This view is supported by the fact that along roadsides *B. ambigua* develops particularly where the surface soil has been removed during the construction of the road, while *Danthonia* is the dominant on more or less undisturbed areas. *Bothriochloa ambigua* may often be seen occupying well-watered areas in table-drains along roadsides

TABLE 7

SUMMARY OF THE CHANGES IN THE NATURAL PASTURES FOLLOWING GRAZING BY SHEEP; WEED INVASION; AND THE POSSIBILITIES FOR SOWN PASTURES UNDER NATURAL RAINFALL

Alliance	Soil Type	Community Following (*a*) Clearing (*b*) "Normal" Grazing	Trends in Composition with Increasing Intensity of Stocking	Weed Invasion	Prospects and Species for Sown Pasture with Natural Rainfall
E. dealbata- *E. sideroxylon* and *E. macrorrhyncha-* *E. rossii*	Shallow soils and rocky sites	(*a*) Shrubs (species variable) with weak develpoment of *Stipa falcata* and *Danthonia* spp. (*b*) Not normally grazed	Not normally grazed		Where sufficient depth of soil and where rainfall >19 in., Wimmera ryegrass, subterranean clover, and *Phalaris tuberosa* could be used provided sufficient phosphate is supplied.
	Deeper soils	(*a*) Shrubs with weak *Stipa falcata* and *Danthonia* spp. (*b*) Small shrubs. Increase in *Stipa falcata* and *Danthonia* spp.	Reduction in shrubs, weakening of *Stipa falcata* and *Danthonia*, increase in annuals On deep sands *Aristida* spp. become dominant		In some areas the use of molybdenum and/or lime may be necessary
E. woollsiana	Light-textured soils	(*a*) *Themeda australis*, *Poa australis*, *Stipa aristiglumis* (*b*) *Stipa falcata*, *Danthonia* spp.	Weakening of *Danthonia*, increase in *S. falcata* Reduction in *S. falcata*, invasion by annuals	*Chondrilla juncea* (serious only in cultivated areas), *Carthamus lanatus*, *Heliotropium europaeum*	In higher-rainfall areas Wimmera ryegrass, subterranean clover, and *Phalaris tuberosa* are successful.
	Medium and heavy-textured soils	(*a*) *Themeda australis*, *Poa australis*, *Stipa aristiglumis* (*b*) *Stipa falcata*, *Danthonia*	Weakening of *Stipa falcata*, increase in *Danthonia* Weakening of *Danthonia*, increase in *Chloris truncata* and annuals Development of scalds		Where rainfall is below 19 in., there are good prospects for the use of Wimmera ryegrass, and some of the early strains of subterranean clover might well prove successful

TABLE 7 (*Continued*)

Alliance	Soil Type	Community Following (*a*) Clearing (*b*) "Normal" Grazing	Trends in Composition with Increasing Intensity of Stocking	Weed Invasion	Prospects and Species for Sown Pasture with Natural Rainfall
E. albens		(*a*) *Themeda australis*, *Poa australis*, *Stipa aristiglumis* (*b*) *Stipa falcata*, *Danthonia* spp.	Reduction in *S. falcata*, increase in *Danthonia* spp. Further reduction of *S. falcata*, decrease in *Danthonia* spp., invasion by *Chloris truncata* and annuals	*Chondrilla juncea* (serious only in cultivated areas), *Carthamus lanatus*, occasionally *Heliotropium europaeum*. On alluvial flats *Silybum marianum*	Wimmera ryegrass, subterranean clover, and *Phalaris tuberosa* could be used throughout this Alliance. It is necessary to supply phosphates, and molybdenum may be necessary in some areas
E. camaldulensis	Well-drained soils, and soils not subjected to long periods of inundation	(*a*) *Poa australis*, *Themeda australis*, *Danthonia* spp. (*b*) *Danthonia* spp. ± *Stipa falcata*	Reduction and even elimination of perennial grasses and invasion by annuals		Wimmera ryegrass and subterranean clover. Phosphatic fertilizers are necessary
Acacia pendula-Atriplex nummularia	Light-textured soils	(*a*) *Kochia aphylla* with *Stipa falcata* and *Danthonia* spp. (*b*) *S. falcata* and *Danthonia* spp.	Reduction of *S. falcata*, increase in *Danthonia*. Reduction of *Danthonia*, increase in *Chloris truncata*, and invasion by annuals Development of scalds	*Carthamus lanatus*	There may be some use for Wimmera ryegrass on both the light- and heavy-textured soils as a competitor for *Hordeum leporinum*
	Heavy-textured soils	(*a*) *Stipa aristiglumis*, *Panicum prolutum*, and *Danthonia* spp. (*b*) No change under light grazing	Reduction of *S. aristiglumis*, *Panicum prolutum*, and *Danthonia* spp. Invasion by *Chloris truncata* and annuals		

within the *E. woollsiana* Alliance. There appear to be two factors favouring its development in these habitats, viz. additional water received as run-off from the roads and other neighbouring areas, and the removal of the surface soil. This species has not been found as a dominant in the pastures of the *E. woollsiana* Alliance, probably because of inadequate water supply.

It has not yet been possible to obtain complete confirmation of this hypothesis regarding the development of dominance by *B. ambigua*. As *B. ambigua* becomes established within a *Danthonia* pasture, the grazing pressure on the Danthonia areas is increased, since *B. ambigua* is unpalatable except during early summer when the young growth may be eaten. Erosion of the surface soil within the *Danthonia*-dominant communities is thereby increased. The erosive force is most commonly surface water during heavy summer rainstorms, and the surface soil removed tends to collect in the *B. ambigua* areas at lower levels. An examination of the soils then reveals the fact that *Danthonia*-dominant areas have lost the A_1 horizon. One such area was examined near Burrumbuttock. If the explanation given above for the development of *B. ambigua* is correct, this species should be actively invading the *Danthonia* pastures, and it may be that *Danthonia* will eventually be able to replace the *Bothriochloa* in those areas where the surface soil has again accumulated. Whether this will take place will depend on the ability of seedling *Danthonia* plants to compete successfully with mature *B. ambigua* and develop in the thick mat of the latter species.

Aristida-dominant pastures are frequently associated with marginal or ecotonal communities, and the soils always appear to have a deep, sandy A horizon of low fertility. In the absence of sheep-grazing the dominant species in the herbaceous stratum is *Stipa falcata,* with *Danthonia* as a subordinate species. The weakening or removal of the *Stipa* and *Danthonia* allows the development of *Aristida,* which, being unpalatable, is not affected by grazing. Continued grazing therefore causes progressively more and more damage to the palatable species until finally a useless pasture, which may be virtually 100 per cent. *Aristida,* is developed (Plate 4, Fig. 2).

Weeds of major economic importance in the pastures are few. *Chondrilla juncea* may frequently be a serious weed in cultivated areas, but is seldom more than a minor constituent of the pastures. Weed species become troublesome only when the perennial constituents of the pastures have been seriously weakened or eliminated by cultivation or heavy grazing. No serious weed development occurs where a vigorous stand of perennials is maintained in the pasture.

The development of improved pastures within the region by the sowing of introduced species has not been practised as widely as might by expected. The use of subterranean clover, Wimmera ryegrass, and *Phalaris tuberosa* could be very greatly extended, and there are distinct possibilities for the use of Wimmera ryegrass in the drier districts even without irrigation. Since Wimmera ryegrass is a winter-growing annual it should prove successful wherever conditions are such that re-seeding is possible.

There are a number of reasons why the establishment of improved pastures has not been more widely practised. Much of the land is held in comparatively

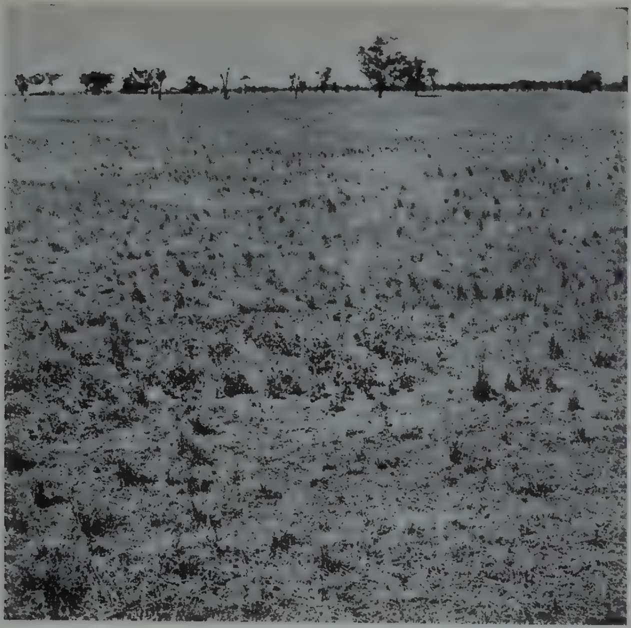

Fig. 1.—*Heliotropium europaeum* (24.ii.1949) as a summer annual in an overgrazed pasture in which *Hordeum leporinum* was the winter dominant. This area has been cleared from *Eucalyptus woollsiana* and *Callitris glauca*.

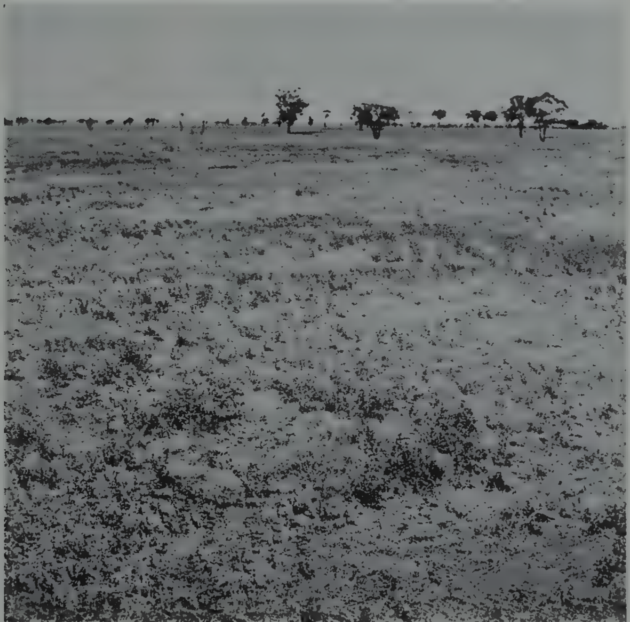

Fig. 2.—Moderately grazed pasture in which *Stipa falcata* is the dominant species. Note absence of *Heliotropium europaeum* except in small depression where *Hordeum leporinum* was the winter dominant. This area adjoins that shown in Figure 1 (24.ii.1949).

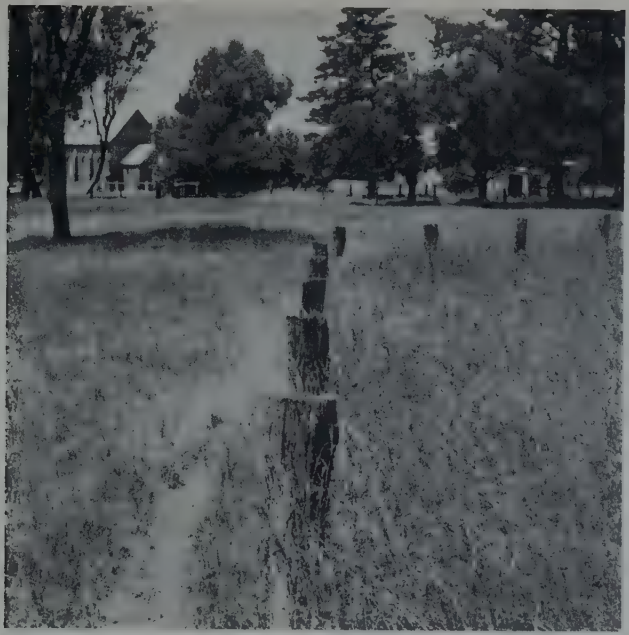

Fig. 1.—*Themeda australis* in cemetery on right, *Danthonia*-dominant pasture in grazed area on left, at Burrumbuttock.

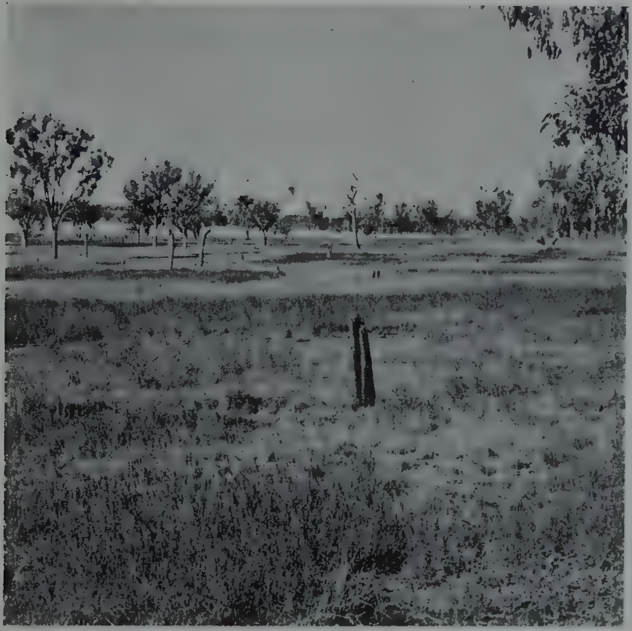

Fig. 2.—Alternes of *Danthonia* and *Bothriochloa ambigua* in pasture developed after partial clearing of *Eucalyptus albens* near Burrumbuttock.

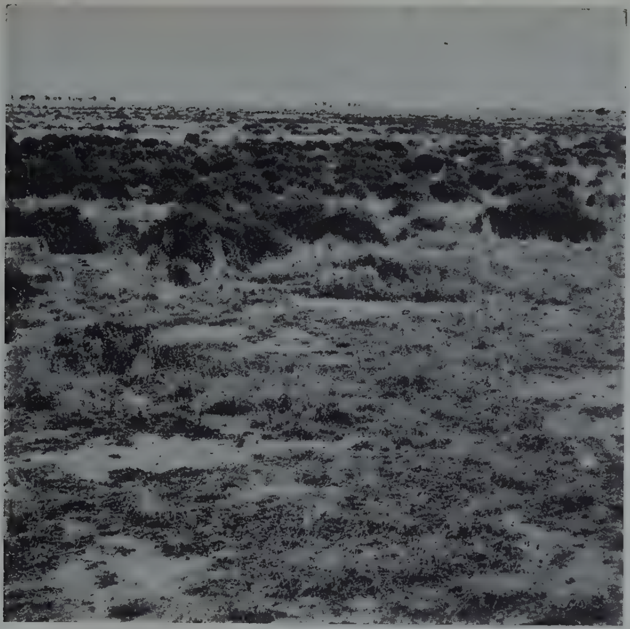

Fig. 1.—*Kochia aphylla* with *Danthonia* sp. in very lightly grazed pasture at "Coonong," near Urana.

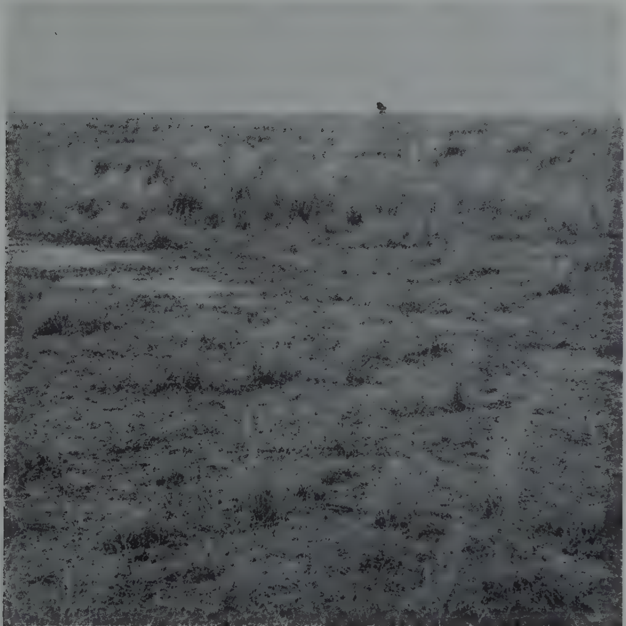

Fig. 2.—*Stipa aristiglumis* dominant in lightly grazed area cleared from *Acacia pendula* and *Atriplex nummularia* on grey clay near Jerilderie.

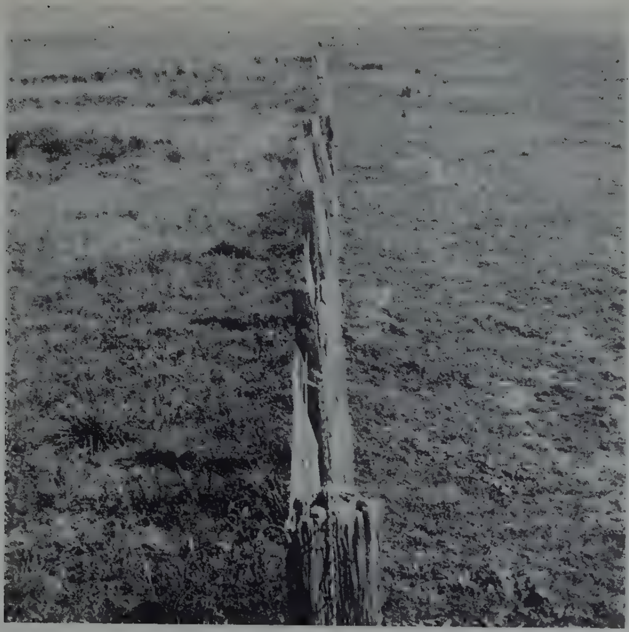

Fig. 1.—The effect of grazing on *Stipa aristiglumis*. On right *Chloris truncata* and annuals are the predominant constituents of the pasture in a heavily grazed area. The lightly grazed area on the left is dominated by *Stipa aristiglumis*. Cleared from *Acacia pendula-Atriplex nummularia* Association, near Narrandera.

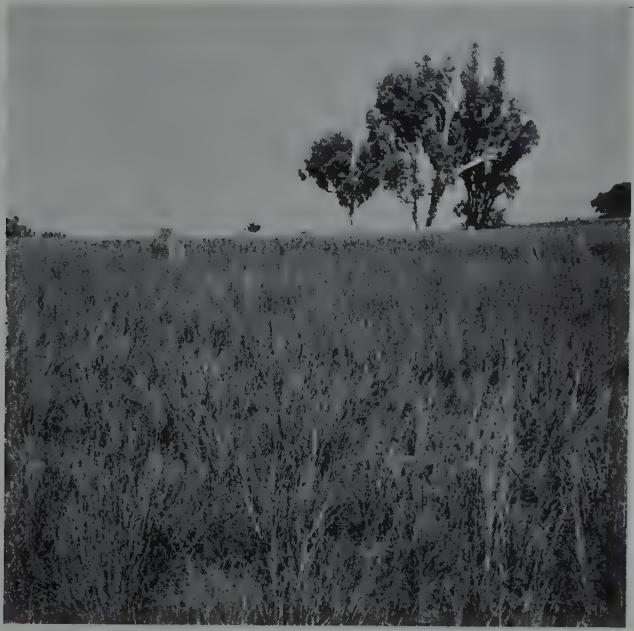

Fig. 2.—*Aristida ramosa* pasture following heavy grazing in a marginal area cleared from *Eucalyptus albens* and *E. dealbata* near Jindera. The soil is a deep sand.

large areas, making it unnecessary for the individual to strive for maximum production to ensure an adequate income. Added to this is the high cost of labour, seed, and fertilizer. Applications of heavy dressings of phosphates are essential in most areas for the successful establishment of introduced grasses and legumes.

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Corrigenda

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Page 51, Figure 2, near bottom of figure, between − 16 Group E and + 5 Group F: *Bassia parviflora* was omitted.

Page 53: Figure 3 should have appeared in the form below:

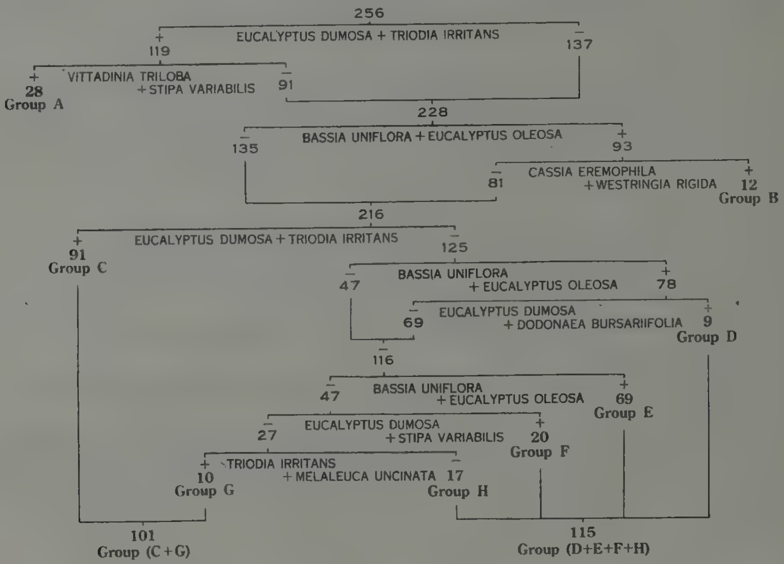
256
EUCALYPTUS DUMOSA + TRIODIA IRRITANS
+ 119
− 137
VITTADINIA TRILOBA + STIPA VARIABILIS
+ 28 Group A
− 91
228
BASSIA UNIFLORA + EUCALYPTUS OLEOSA
− 135
+ 93
CASSIA EREMOPHILA + WESTRINGIA RIGIDA
− 81
+ 12 Group B
216
EUCALYPTUS DUMOSA + TRIODIA IRRITANS
+ 91 Group C
− 125
BASSIA UNIFLORA + EUCALYPTUS OLEOSA
− 47
+ 78
EUCALYPTUS DUMOSA + DODONAEA BURSARIIFOLIA
− 69
+ 9 Group D
− 116
BASSIA UNIFLORA + EUCALYPTUS OLEOSA
− 47
+ 69 Group E
EUCALYPTUS DUMOSA + STIPA VARIABILIS
− 27
+ 20 Group F
TRIODIA IRRITANS + MELALEUCA UNCINATA
+ 10 Group G
− 17 Group H
101 Group (C+G)
115 Group (D+E+F+H)

Fig. 3.—Stages in the separation and recombination of groups by procedure III.

Page 55, Figure 4, at bottom of figure, between − 26 Group E and + 17 Group F: *Triodia irritans* + *Dodonaea bursariifolia* was omitted.

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